THE
VERTEBRATE SKELETON
FROM THE DEVELOPMENTAL
STANDPOINT

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BY

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WITH 324 ILLUSTRATIONS

PREFACE

This volume aims to give an outline of Vertebrate osteology, tracing the skeletal elements from their early appearance to the adult condition, for only by ontogeny can homologies (or their lack) be ascertained in the various groups. Since knowledge of the adult structures of higher Vertebrates is best obtained by comparisons with lower forms, greater stress has been laid on Ichthyopsida and on reptiles than upon birds and mammals, which have been more adequately treated elsewhere than have lower groups. There is also reference to extinct forms, as these frequently throw light upon the living species. The work is intentionally descriptive, and no attempts have been made to trace lines of descent, although here and there hints are given of the relations of groups. While teeth are really parts of the skeleton, they are largely ignored here, because of inadequate knowledge on the part of the author and from lack of space. Facts concerning them are readily accessible in the works of Owen, Tomes, Cope, Osborn, Röse and others.

The writer is conservative in nomenclature, using the terminology of morphological literature rather than the names advocated by the worshipper of priority. *Acanthias Amia*, and *Esox* are used all through anatomical literature and nothing is to be gained by the substitution of *Squalus*, *Amiatus* and *Lucius*. Nor is science benefitted by adopting the etymological absurdity *Lepisosteus* or the typographical error *Ambystoma*, almost immediately corrected by Agassiz.

The terminology of the 'BNA' (Basle Nomina Anatomica) has been followed in most cases, but occasionally (*e.g.*, transverse process, obturator foramen) this introduces confusion, while sometimes terms must be used for parts lacking in the adult human skeleton, to which the BNA is restricted. In recent years there is a tendency to give new names to parts already well named; the familiar nomenclature is retained here. A few years ago, as a result of misinterpretation of parts, the name paraquadrate was given to the bone here called squamosal, while one author gave the

name operculare (already in use for an element of the gill-cover) to both the splenial of the lower jaw and to the stapedial plate of the ear bones. Certain terms (*e.g.*, epiotic for a roofing bone of the skull) have been discarded as they imply homologies which do not exist. Few new terms have been introduced here, the most notable case being for the parts which form the definitive vertebra, for which no names showing the actual relations were available. These examples illustrate the reasons for the terminology employed.

The appended bibliography of nearly a thousand books and papers has been selected from thousands of cards. To economize space, most titles have been abbreviated, but in such a way as to give some idea of the contents of the article.

Acknowledgments are due to the University of California and to its departments of Zoology and Anatomy for many facilities afforded me, and especially to Professor Joseph Grinnell for the freedom of access to the skeletons in the Museum of Vertebrate Zoology under his charge.

<div align="right">J. S. Kingsley.</div>

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VERTEBRATE SKELETON

INTRODUCTION

As included here, the skeleton of Vertebrates embraces all harder protective and supporting structures derived wholly or in part from the mesenchyme, one of the two divisions of the mesoderm. This definition excludes such protective features as hair, feathers, scales of snakes and lizards, and the like, which are formed by the ectoderm, also some, the same in origin (hoofs of mammals, beaks of birds) which are firmer than many true skeletal parts. To these mesenchymatous parts must be added the notochord, derived from the entoderm.[1]

Embryology.—As implied above any part of the mesenchyme is a potential source of skeletal parts, hence it is necessary to know the distribution of the layer, especially in the embryo, to follow the course of skeletal formation. So there follows a brief and very generalized resumé of some features of embryology. In Vertebrates, gastrulation and the early differentiation of the germ-layers, is a complex process (especially so in Amniotes) and details are not

[1] The notochord, characteristic of all Chordata, occurs on no invertebrate. It extends from the tip of the tail forwards, in Vertebrates, to the hypophyseo-infundibular region, a little behind the tip of the head. It forms an axis around which the vertebræ and part of the skull develop. More or less of it persists through life in the lower groups, but it almost wholly disappears from Amniotes before the adult stage is reached. In lower Vertebrates and in Tunicates and *Amphioxus* it is clearly a product of the entoderm (fig. 1), being cut off from the mid-dorsal line of the archenteric wall. The fusion of germ layers is so complete in Amniotes in the early stages that students have derived the notochord from each of the three layers. If this structure be the same in all Vertebrates, its origin must be the same in all, otherwise there is an enormous difficulty in reconciling its homology in lower and higher groups.
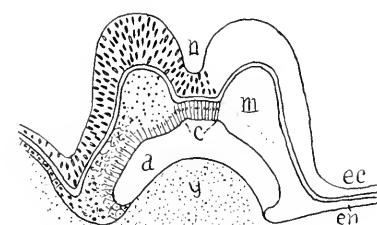

FIG. 1.—Section of *Acanthias* embryo before formation of somites, showing notochordal cells as part of entoderm. *a*, archenteron; *c*, notochordal cells; *ec*, ectoderm; *m*, forming mesothelium; *n*, neural groove; *y*, yolk.

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necessary here as they are given in every text-book of embryology.
More important is the differentiation of the skeletal-forming (sclero-
blastic) tissues and their distribution so that the steps in the forma-
tion of the skeletal parts may be followed.

In the early stages of all Vertebrates three germ layers are present
—ectoderm and entoderm, with the third, the mesothelium between
them. At first the mesothelium forms pairs of closed sacs, the cavi-
ties of these being the **cœlom.** One face of each sac—the **somatic**—
is turned towards the ectoderm, the other (**splanchnic**) faces the
entoderm. The dorsal part of each cœlomic sac becomes divided
by transverse incisions into a series of quadrate bodies (**myotomes**)
which a little later separate from
the lower part of the sac, each now
forming a closed vesicle, its cavity
being the **myocœle.**

In the lower and simpler Verte-
brates these three layers constitute
the whole of the early embryo.
(*Amphioxus* never has more than a
slight differentiation of the fourth
(mesenchymatous) layer.) At first
these layers are distinct, being sepa-
rated by an actual or potential space,
the remains of the archicœle of the
cleavage stage of the egg.

The fourth layer, the **mesen-
chyme,** owes its cells to all of the
other layers, but the greater part of
them—and practically all which are
concerned in skeletal formation—come from the myotomes. A part
of the splanchnic wall of each myotome (fig. 2) buds cells into the
space between the rest of the mesothelium and the axial structures
(blood vessels, notochord, and central nervous system), these cells
forming the mesenchyme for most of the axial skeleton. At first
these cells form groups (**sclerotomes**), metameric like the myotomes
from which they arise.

A second source of mesenchyme lies in the somatic myotomic
walls, the cells of which lose their epithelial character, and, lying
just beneath the ectoderm, form the deep layer (**corium**) of the skin,

FIG. 2.—Section of *Lacerta* embryo,
showing proliferation of mesenchyme
from splanchnic side of myotome to form
scleroblasts. *a*, aorta; *l*, limb-bud; *m*,
muscle-forming part of myotome; *n*,
notochord; *sk*, sclerotomic part of
mesenchyme.

the tissue which gives rise to many of the dermal (membrane) bones and other skeletal bodies near the surface of the animal.

With further growth, the mesenchyme from all sources invades all spaces between other structures, forming a continuum which has been called the **membranous skeleton,** but as this is illy defined, and as a large part of it never becomes truly skeletal, it needs no further mention, save to say that all true skeletal parts—cartilage and bone—are formed within its limits, and that wherever it occurs there is the potentiality of skeletal formation.

More definitely, the chief locations of skeletogenous tissue in the trunk are the following (fig. 3); Between the ectoderm (epidermis)
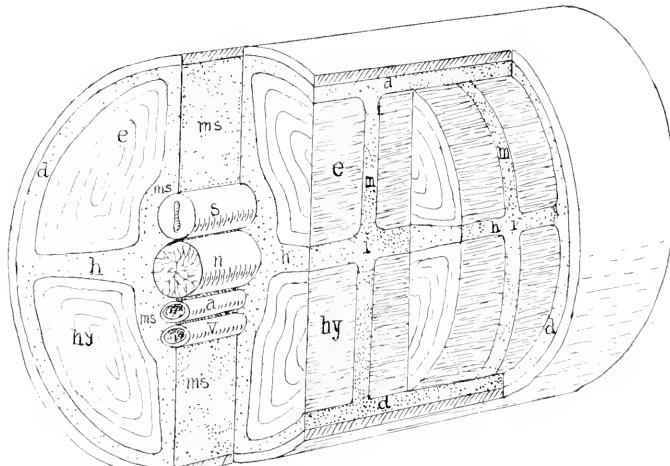
FIG. 3.—Location of skeletogenous tissue in caudal region. *a*, caudal artery; *d*, corium; *e*, epaxial muscles; *h*, horizontal septum; *hy*, hypaxial muscles; *i*, intersection of (*m*) myosepta with horizontal septum; *ms*, median septum; *n*, notochord; *s*, spinal cord; *v*, caudal vein.

and the trunk muscles is the corium. This is connected at the middle line, above and below, by a vertical median septum of mesenchyme extending between dorsal and ventral sides of the trunk, passing on either side of the spinal cord, notochord, dorsal aorta, and the chief viscera located in the body cavity. The muscles of either side of the embryo (also of adult fishes) are segmented, the segments (myotomes) being separated by vertical partitions of mesenchyme (**myosepta**) extending from corium to the median septum. The myotomes of either side are divided into dorsal (**epaxial**) and ventral (**hypaxial**) muscles by a similar horizontal septum, also

extending from the median septum to the skin. In the tail the relations are much the same, except that the body cavity and its viscera are absent.

In the formation of the skeleton three different conditions are recognized. The first is the membrano-skeleton, just noticed, most of which becomes transformed into several tissues, grouped by histologists as connective tissues. The other conditions are the cartilaginous and the bony (osseous) skeletons which differ markedly in character. There are less differences between the bones which form the internal skeleton and the scales of the dermal skeleton, there being a close connection between these, as it is probable that most, if not all bones had their phylogenetic origin directly or indirectly from dermal ossifications.

The corium is concerned chiefly in the formation of dermal scales, but in the head it gives rise to certain of the cranial bones. The median septum has to do with the development of the vertebral column, skull, sternum and some other structures of less importance. Ribs may form at the intersection of myosepta and the horizontal septum. The skeleton of the median fins of fishes arises in the dorsal and ventral extensions of the median septum; that of the paired appendages is not so easily located in the scheme, although, like the rest, it is mesenchymatous in origin.

Dermal scales are calcified structures which, as the name implies, arise in the deeper layer (**derma** or **corium**) of the skin. They have a special importance since from them teeth and membrane bones have been derived, and from the further possibility that all ossification had its origin from them. Cartilage is never concerned in their history; they arise as direct ossifications in the corium, often with additions from the ectoderm which have no significance in the general morphology of the skeleton.

The typical dermal scale, the **placoid scale,** occurs in the skin of Elasmobranchs, all other dermal scales being thought to be derivatives of these. Hence an outline of their development is given, details of structure being found in the section dealing with the dermal skeleton in different Vertebrates (p. 10).

The first step in the development of a placoid scale is a multiplication of mesenchyme cells in restricted areas of the corium, immediately beneath the ectoderm. These cell aggregates thicken the corium in spots, resulting in the elevation of the overlying ectoderm, this

affecting most its basal (germinal) layer, these elevations being occupied by mesenchyme (fig. 4). The cells of these protrusions now secrete an organic substance (ossein) on their outer surface, which is impregnated with calcareous salts, thus forming the basal substance (**dentine**) of the scale. From this as a centre, the deposition of dentine extends laterally on the corium as far as the modified mesenchyme cells occur. The result is a basal plate formed by the distal parts of the condensed mesenchyme, with a central spine extending from the centre into the elevated part of the ectoderm. Basal plate and spine differ in that no cells are included in the dentine of the spine, while they are embedded in the substance of the basal plate. The cells of the germinal layer of the epidermis become columnar, forming the **enamel organ** which secretes from its deeper
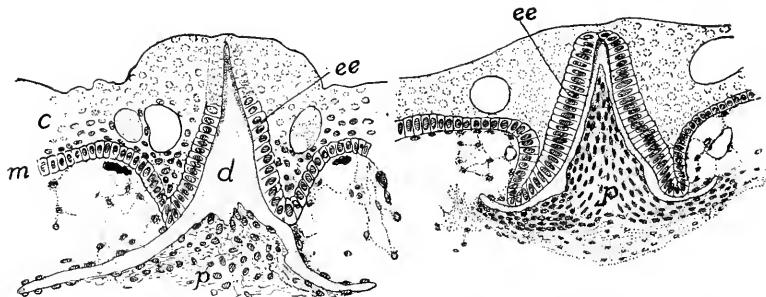

FIG. 4.—Sections of developing scales of *Acanthias*. *c*, stratum corneum; *ee*, enamel organ secreting enamel (densely stippled); *d*, dentine; *m*, rm. germinal layer; *p*, pulp.

surface a very dense calcareous layer (**enamel**) which covers the spine, but not the basal plate. A placoid scale is therefore a product of both mesenchyme and ectoderm. By continued growth the tip of the spine protrudes through the skin, while the interior of the spine has a **pulp cavity,** occupied with the mesenchymatous 'pulp' together with minute blood vessels and nerves.

A union of several such scales would result in an osseous plate, which, with the loss of spines and enamel, would be very like the bony plates on the heads of many primitive fishes and would account for the membrane bones soon to be described.

BONE.—Two types of bone are recognized, differing in development, although indistinguishable in the adult, except by following their history. One is the **dermal** or **membrane bone** which arises as a direct ossification of mesenchyme, without any cartilage in its

history. The other, **cartilage bone,** is preformed in cartilage, which is later torn down, its organic substance (**chondrin**) being replaced by ossein with a large amount of lime salts. The distinction between the two kinds of bone is of great importance in determining homologies (or their lack) in bones occupying the same relative positions in different Vertebrates.

Cartilage begins by an accumulation of mesenchyme cells, its early stage (procartilage) being readily recognized in the stained section by the closely packed nuclei with a small amount of protoplasm around them. As development proceeds each cartilage cell secretes chondrin around itself, the amount of this increasing with time, so that eventually the cells are separated by a considerable amount of chondrin, the so-called **matrix.** This process increases the size of the cartilage mass, the growth of which is also effected by the division of the cartilage cells as well as by the addition of cells from the surrounding mesenchyme.
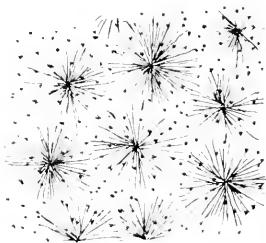

FIG. 5.—A bit of calcified cartilage, with radiating spicules of calcic carbonate.

When a cartilage element has attained its definitive form, the mesenchyme touching it becomes a fibrous connective tissue, forming an envelope (**perichondrium**), which connects adjacent cartilages, affords attachment for muscles and ligaments and carries blood vessels to nourish the cartilage, although no vessels enter the matrix.

In many cases the cartilage thus formed remains unmodified and constitutes the **hyaline cartilage** of histology. Or it may be strengthened by fibres (elastic or non-elastic) in the matrix. In adult Elasmobranchs, and especially the larger species, a deposition of lime salts occurs in the matrix, this being most marked in the later and outer layers, the result being calcified cartilage, most abundant on the outer surface of the skull, vertebræ, etc. (fig. 5). Calcified cartilage differs from bone in the absence of canals and canaliculi, in having no blood vessels in the matrix and in not having the cells in layers (lamellæ), while the calcareous salts form irregular patches of radiating spicules (fig. 5). In Myxinoids different kinds of cartilage—true and pseudo—each with hard and soft varieties—are recognized, for details of which reference should be made to special papers.

Cartilage Bone.—Cartilage persists as such in adult Cyclostomes and Elasmobranchs and in some parts of all Vertebrates, the amount remaining being less in the higher groups. Usually more or less of it is converted into cartilage bone (**autostoses**). This occurs in two ways. In the lower Vertebrates **perichondrial ossification** predominates, the inner cells of the perichondrium becoming bone-formers (**osteoblasts**) which lay down bone on the outer surface of the cartilage, the process gradually invading the deeper parts. In the higher Vertebrates **endochondral ossification** prevails. Blood vessels from the perichondrium invade the cartilage, dissolving the matrix and setting its cells free, these now changing to osteoblasts which arrange themselves around the blood vessels, and secrete the ossein and lime salts of bone. With either type of ossification the perichondrium becomes the **periosteum.**

Membrane bones (**allostoses**) arise without a cartilage stage, the connective tissue cells secreting ossein and lime directly, some cells becoming osteoblasts, those surrounding them forming the periosteum. Many membrane bones, especially in the skull, are regarded as having arisen by the fusion of the basal plates of placoid scales or their homologues, teeth, the fusion of such parts being well marked in the growth of dermal bones of Ganoids (*Polypterus, Acipenser*). The participation of teeth occurs in the oral region. The cavity of the mouth

FIG. 6.—Vomer of *Amblystoma* (Hertwig) showing bone formed by fusion of bases of teeth.

is largely lined by an involution (**stomodeum**) of the skin which has carried with it scales which have become teeth, the development of teeth and placoid scales being practically identical. In many animals it is evident that at least some of the bones near the oral surface have been formed by the fusion of the bases of teeth (fig. 6). In the higher groups this bone formation has been emancipated from the teeth, the latter not appearing until after the bones are well outlined. There are also membrane bones which arise as ossifications of ligaments, like the patella of mammals and the ligamentary bones in the 'drumstick' of the turkey. A third type of membrane bone occurs in fishes where the lateral line organs are surrounded by bony tubes (fig. 100), especially those parts of the canal around the eye.

Ossification of both kinds of bone proceeds from one or more **centres** in a single bone. In many cases each centre indicates a separate ancestral bone, and where there are two or more centres a bone complex is indicated. But this is not always the case, although there is no rule definitely deciding the matter; comparisons with other forms are often necessary to settle a question.

Bone complexes are common. These may be unions of two or more membrane bones, or of cartilage bones, or, less common, of cartilage and membrane bones into a single bone in the adult. There are also supernumerary bones, of little morphological significance, in various places. Such are the **Wormian** (**sutural**) bones of the human skull, the patella and pisiform in the limbs, etc.

The distinction between membrane and cartilage bones must be employed with great care in tracing homologies. It is maintained with plausibility that all ossifications had their beginnings with membrane bones and that these have come from dermal scales. It is common in Teleosts to find bones of the two types intimately associated, true cartilage bone being formed within the perichondrium of a cartilage while a membrane bone develops on the outer surface of the same membrane, the two bones fusing later to a single element. It is not possible to determine by structure alone whether a bone be cartilaginous or membranous in origin; this can only be settled by following the development.

The question which is older, membrane bone or cartilage, has not been settled. In the most primitive Vertebrates (Cyclostomes) cartilage occurs, but nothing resembling bone. In the development of the higher vertebrates cartilage always appears before bone. On the other hand the oldest fossil fishes known have an external skeleton of bony plates, and in Ostracoderms no internal skeleton has been found. In higher Vertebrates membrane bone appears in ontogeny long before there is any ossification of cartilage.

The nomenclature of bones is based upon human anatomy, and so far as possible the names of the parts in man are transferred to those of lower Vertebrates. Sometimes this is easy, but again, more or less difficulty is encountered. Some of the bones of the adult human skull are represented by several perfectly distinct bones in the lower groups. Then there are cases where a bone present in a lower form has been completely lost, no representative of it being found in man or any mammal. So far as possible the names of the bones of the lower groups are those of man or are based upon actual or supposed homologies, but not all questions have been settled as to homologies, as will be apparent in the following pages.

The bones (and cartilages) of the skeleton are connected with each other in different ways, some permitting more or less motion while others result in fixed joints. The connecting substance may be cartilage or ligament, and where there is great mobility a true joint (**diarthrosis**) is formed. In the development of diarthroses there is

usually a cavity between the two elements filled with a (**synovial**) fluid which lubricates the articulating surfaces. Where there is little or no motion the connecting substance is less in amount, and special names are given to the different conditions. Connexion by ligament is **syndesmosis,** by cartilage, **synchondrosis.** In the skull many of the bones are very close together, the opposing edges interdigitating by saw-toothed margins, cases of **suture.** When two bones are so closely united in the adult that no trace of suture or other indication of primitive distinctness persists, it is called **synostosis.**

THE SKELETON

For convenience of treatment the skeleton is divided into **dermal** or **exoskeleton,** and **internal** or **endoskeleton.** The first is developed exclusively in the skin, especially in the corium. The endoskeleton belongs in the deeper mesenchymatous tissues; much of it has a cartilage stage, more or less cartilage persisting through life. Most of the membrane bones of the endoskeleton, and especially those of the skull, are clearly of dermal origin in the lower Vertebrates, but they are so closely related to the deeper structures that they are dealt with along with the endoskeleton.

The endoskeleton readily falls into **axial** and **appendicular** portions. The axial is restricted to the head, body proper, and tail, and includes the vertebral column, skull, ribs and breast bone, all lying in or near the body axis. The appendicular skeleton includes the parts in the appendages (median and paired fins, arms and legs) and the skeletal arches or girdles in the trunk, which support the paired appendages. In the following pages the order of this outline will be followed, both in the general accounts and in the description of parts in the separate classes and orders.

EXOSKELETON

The exoskeleton consists of calcified structures (primitively scales) which arise as direct ossifications in the corium, no cartilage appearing in their history. To the mesenchymatous parts there may be added other calcified portions secreted by the basal layer of the epidermis as described above (p. 5). This dermal skeleton is best developed in fishes and reptiles, is very scanty in mammals and recent Amphibians, and no traces of it appear in Cyclostomes or birds.

Apparently the exoskeleton arose as protective structures in the skin. It never formed large sheets as in Arthropods, because of the different relations of the muscle segments. Its elements are small, separate from each other, some of the lines between them coinciding with the myosepta which run obliquely to the major axis of the body. Examination of any ordinary fish will show the typical arrangement of the scales.

ELASMOBRANCHII

**Scales.**—The placoid scale of Elasmobranchs, the development of which was outlined above, although complex in structure, is regarded as close to the primitive element and as furnishing the starting point from which all other dermal skeletal parts have been derived. Each placoid scale consists of a basal plate of varying size (largest in skates), with a hollow spine (fig. 7) directed backwards, arising from its outer surface. Basal plate and the inner part of the spine are formed of dentine which differs from bone chiefly in lacking bone cells in most of its substance. The outer surface of the spine is covered by a denser calcified coat (**vitrodentine**), commonly called enamel, but not certainly such. The cavity of the spine contains mesenchyme (pulp), blood vessels and nerves. It is frequently branched and connects with the corium by one or more openings in the dentine.

Fig. 7.—Longitudinal section of placoid scale. *d*, dentine; *e*, enamel; *p*, pulp cavity.

Considerable differences occur in form and size of Elasmobranch scales. They are small in most Euselachii, with rhomboid basal plate and a spine which projects through the epidermis. Most Batoids (skates) have them larger, irregularly placed and have a stronger spine. These reach their extreme in the 'teeth' on the sides of the saw of sawfishes (Pristidæ). *Torpedo*, like most electric fishes, lacks all scales. The only scales of Holocephals are those on the peculiar frontal horn and the claspers of the male and in the greatly hypertrophied spine at the front of the dorsal fin. It is noteworthy that the embryo of *Callorhynchus* (Holocephal) has rows of scales which lack enamel, upon the occiput and scattered elsewhere.

Ostracoderms may be mentioned here. The most primitive members of the group have spines without conspicuous basal plates. In other species fusion of similar scales with basal plates have formed the armor covering the anterior part of the body, traces of spines sometimes showing on the outer surface.

GANOIDS.—The scales of typical Ganoids consist of two layers. The basal layer (usually called dentine, better, **isopedin**) resembles true bone in having bone cells. The superficial layer (**ganoin**) is denser and has a polished surface. Both layers are formed by the corium and neither can be compared to the enamel of the placoid scale.

In the development of the scales of *Lepidosteus* the basal part is laid down in the corium (fig. 8); it is at first circular in outline, and each scale remote from the others. Then the basal layer of the epidermis deposits a true enamel as numerous spines, these separated from the dentine by a layer of mesenchyme which later secretes the ganoin, while spines and enamel are lost. It is a question whether each ganoid scale equals one or several placoid scales.
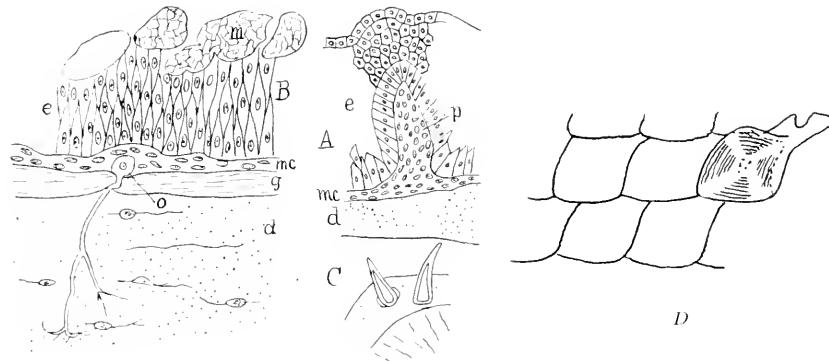

Fig. 8.—*A, B, C*, Development of scale of *Lepidosteus* (Nickerson, '93); *D*, adult scales (Butschli, '10). *A*, early stage with development of organ for spine (compare with development of placoid scale); *B*, later, with developing ganoin; *C*, margin of scale of young fish showing two spines. *d*, dentine layer; *e*, epidermis; *g*, ganoin; *m*, mucus cells; *mc*, mesenchyme (corium) overlying dentine; this develops the ganoin; *o*, odontoblast; *p*, pulp of spine.

In the adult *Lepidosteus* the scales are enlarged to rhomboid plates which slightly overlap, forming a dense armor, the strength of which is increased by an interlocking process on the anterior margin of each scale (fig. 8, *D*). *Polypterus* (fig. 239) has scales superficially much like those of *Lepidosteus* in appearance and arrangement, but differing in details (Goodrich, '07). The scales of sturgeons (Chondrostei) are large plates of bone arranged, in living species, in five longitudinal rows, the scales of the mid-dorsal row being the largest. These arise as ossifications in the corium without any enamel or ganoin, reaching the surface later by loss of the overlying corium and epidermis. Besides these larger scales there are smaller ones between the larger rows. *Polyodon* has scales in

the young which are lost in the adult (except at the base of the tail), unless scattered irregular calcareous bodies are degenerate scales. The scales of *Amia* lack all ganoin and, in arrangement and appearance, are very similar to the cycloid scales of Teleosts (infra). At the bases of the fins of Ganoids (and a few Teleosts) are modified scales known as fulcra.

TELEOSTS.—Many but not all eels and scattered members of other groups lack scales, but most of the others have them arranged in rows in line with the myotomes (occasionally two or more rows to a myotome), the successive rows overlapping like shingles, from in front backwards (fig. 9). In their development mesenchyme cells become aggregated at regular intervals, the interior cells of each group becoming specialized as scleroblasts which secrete a thin

Fig. 9.—Relations of teleost scales (black) to layers. *c*, corium; *e*, epidermis.
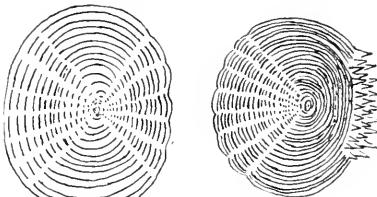
Fig. 10.—Cycloid and ctenoid scales.

layer of organic matter from their inner ends. This secretion increases with age by the deposition of successive layers, each new layer extending beyond the margin of the last, the result being a series of lines of growth. At first these scales are remote from each other, but with growth, the anterior margin of each extends slightly inwards, the posterior outwards, resulting in the characteristic overlapping (fig. 9). Usually, but not always, the scales contain bone cells. The inner layers are thin and flexible, the outer more or less calcified.

Most Teleost scales (fig. 10) may be grouped as either cycloid or ctenoid, but the two types intergrade and both may occur on the same fish. **Cycloid scales,** occurring in Physostomi and many Acanthini, are approximately circular and are marked by radiating lines and concentric lines of growth, the centre being a little behind the middle of the scale. **Ctenoid scales** have the same lines and also radiating series of spines on the outer surface, these covering the whole side or only the posterior portion. Some Siluroids have denticles (with pulp cavities) in the skin, recalling the larval *Lepidos-*

teus (p. 11): some others have the body enclosed in an armor of large plates, concerning the history of which little is known. In other Teleosts there is far less regularity, peculiarities occurring in Plectognaths, Lophobranchs and some Acanthopterygii, for details of which reference should be made to systematic ichthyologies.

DIPNOI.—In appearance at least, the scales of modern Dipnoi are much like those of typical Teleosts.

AMPHIBIA.—Scales are uncommon in modern Amphibia, but were the rule in Stegocephals where they were usually restricted to the ventral sides of the body, sometimes extending to the limbs and
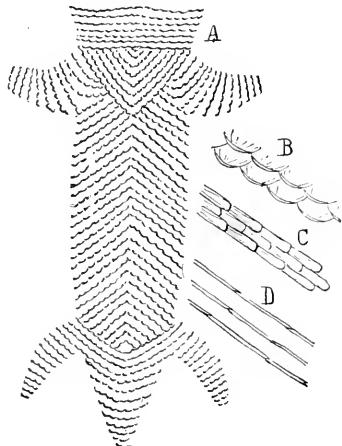

FIG. 11.—Ventral plates of Stegocephals (Credner in Zittel). *A, Branchiosaurus; B,* details of same; *C,* of *Archegosaurus; D,* of *Petrobates.*
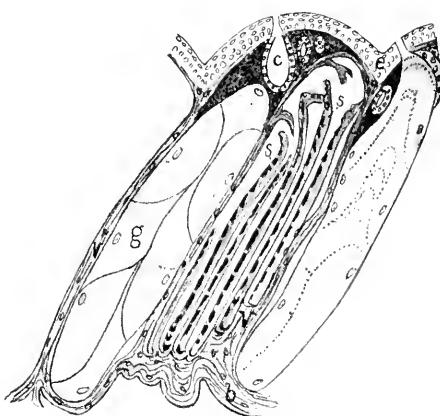
FIG. 12.—Section of skin of a body ring of *Epicrium* (Sarasins, '87). *b,* basal layer of corium; *c, g,* glands; *e,* epidermis; *s,* scales, the black spots the squamulæ; the head to the left.

rarely to the back. Apparently scales of a cycloid appearance were the most primitive and were arranged in oblique overlapping rows, converging forwards (fig. 11). In the more specialized genera the scales were slender and rod-like with gaps between the rows. It is suggested that the gastralia of reptiles (p. 16) and at least some of the plastral bones of turtles have been derived from scales similar to the ventral armor of Stegocephals.

Some Gymnophiones (fig. 12) have numerous scales embedded in pouches in the skin, several scales in each pouch. Each scale is two layered, the outer surface divided by reticulate lines into small circular areas (**squamulæ**) of uncertain significance. The scales are

slightly ossified.   Urodeles, like most Anura, lack scales, but a few of the latter order (*Ceratophrys, Brachyocephalus*) have plates of bone in the skin of the back, sometimes ankylosed to the spinous processes of the vertebræ.   Possibly these are cœnogenetic.

REPTILIA.—Most reptiles have a more or less developed exo-skeleton which may be divided into two groups of structures, the dermal scales developed in the corium, and the deeper gastralia. Dermal scales were lacking in Ichthyosaurs (except a few ossicles on the margin of the dorsal fin), Sauropterygia, Pythonomorphs, snakes,[1] most lizards and Dinosaurs and all Pterosaurs.   When present, the scales are developed in the skin, and in the living species are usually covered by a horny cuticle, mesenchyme intervening between the two.   They are usually isolated plates, but frequently they are articulated into a nearly complete armor, represented in the modern Crocodilia by rows of plates embedded in the skin of the back (in *Jacare* and *Caiman* of the belly also).   In some extinct Crocodilia they overlapped like fish scales, in others they were large articulated plates over the whole body.   Many skinks and some Ascalabotæ have ossifications in the skin, remnants of the ancestral armor, but most lizards and *Sphenodon* lack dermal scales.

Of most of the extinct groups little need be said, except that some of the Stegosaurian Dinosaurs had, not only scattered ossicles, but enormous plates and spines—some plates over a yard across—extending as an enormous comb the length of the back, while *Pola-canthus* had the lumbar region enclosed in a complete coat of fused scales.

Most species of CHELONIA have the dermal skeleton greatly developed, forming, with the ribs, a case in which, in some genera, head and tail may be retracted.   This case consists of a dorsal **cara-pace** and a ventral **plastron,** the two sometimes united at the sides by ligament, sometimes this has ossified and carapace and plastron are firmly united by suture or fusion.   When fully developed the carapace (fig. 13, *A*) consists, besides of ribs, of a series of median ossicles.   The most anterior of these, the **nuchal plate,** is free from the axial skeleton, while the eight following **neural plates** are fused to the spinous processes of the underlying vertebræ.   The median series is completed behind by one or more **pygal plates,** much like the nuchal.   Each neural plate is joined on either side by a **costal**

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[1] The 'scales' of snakes are purely epidermal structures.

plate which extends to the margin of the carapace and is fused to the rib below. The margin of the carapace is formed by a series (11 to 12) of **marginal plates,** passing in front and behind into the nuchal and pygal. Outside of this osseous carapace are cuticular horny plates which correspond to neurals and costals neither in number or position.

The plastron normally consists of nine bones (also with cuticular plates): an anterior unpaired **entoplastron** (fig. 13, B) succeeded by a pair each of **epi-, hyo-, hypo-** and **xiphiplastra.** Occasionally (Dermochelydæ, Cinosternidæ) the entoplastron is lacking, while some have a **mesoplastron** intercalated between hypo- and hyo-plastra of either side.
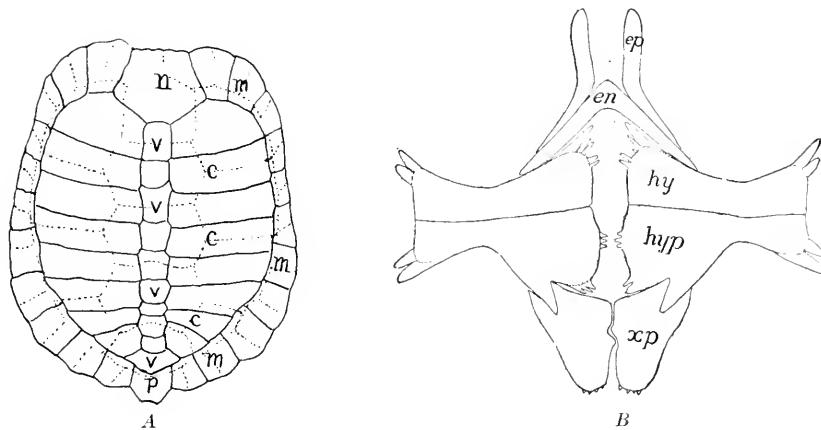

FIG. 13.—Carapace (A) of *Chelopus insculptus* (Parker, '01) and plastron of *Trionyx* (B). *c*, costals; *en*, endoplastron; *ep*, epiplastron; *hy*, hyoplastron; *hyp*, hypoplastron; *m*, marginals; *n*, nuchal; *p*, pygal; *v*, vertebrals; *xp*, xiphiplastron.

From this typical (not primitive) condition many variations occur. Usually the costals of either side extend to the marginals, but in some sea turtles and in Trionychidæ the costals do not extend as far as do the ribs, leaving gaps between them and the marginals. In still others the costals are narrower, leaving gaps from marginals nearly to the vertebral column, while in some Trionychidæ (which lack cuticular scales) marginals may be absent. The Dermochelydæ afford a problem. The plastral bones are small, forming a ring with a gap in the centre, marginals are lacking and costals are reduced. In the skin overlying these last are numbers of polygonal plates which articulate with each other, and are arranged in longitudinal rows. The plates in seven of these rows are larger than the others and each plate is keeled. Some Emyidæ have the anterior and posterior plastral plates hinged to the others and are capable of being closed against the carapace (box tortoises).

There is great uncertainty as to the homologies of these plates in the Chelonian skin. The ossicles of the Dermochelydæ certainly belong to the dermal skeleton, and the same probably holds for marginals, nuchals and pygals. Costals and neurals are held by some to belong to the axial skeleton. The plastral bones are supposed to be derived from the ventral scales of some Stegocephal-like form, but no intermediate stages are known. The possible homology of entoplastron and epiplastra with episternum and clavicles will be mentioned later.

In CROCODILIA and *Sphenodon* of living forms, and in the extinct Rhynchocephals, Ichthyosaurs, Plesiosaurs, Phytosaurs, Thalattosaurs, some Dinosaurs and all Pterosaurs another series of dermal bones, the **gastralia,** occur; they are also called **abdominal ribs** and **parasterna.** They are rib-like in appearance and occupy the gap between the last true rib and the pelvis. They lie in the rectus muscles of the abdomen, are not connected with the vertebræ and in their development no cartilage appears. They are composed of two or more overlapping bones on either side, those of the two sides converging forwards. The number varies from one to a somite in Crocodilia (fig. 14), two in Sphenodon, up to six in some fossils. These facts all militate against their being ribs; the usual interpretation is that they are the representatives of the abdominal armor of Stegocephals (p. 13).

AVES.—With the exception of the ancient *Archæopteryx,* dermal bones are unknown among Aves. *Archæopteryx* has gastralia in the abdominal walls, but no other dermal bones.

MAMMALIA.—Gastralia are lacking in all mammals, and dermal bones occur only in Edentates and Cetacea. Some Edentates have an armor of dermal scales around the body, arranged either in transverse rows (armadillos) or as a mosaic of polygonal plates (*Glyptodon*), the ossicles in both extending on head, limbs and tail. In armadillos the scales arise from isolated centres in the corium, these meeting later, with partial obliteration of the hair. The arrangement differs in the several genera.
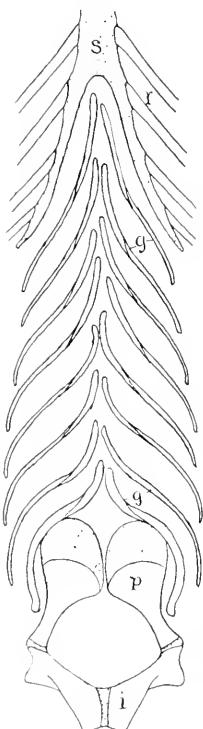
FIG. 14.—Gastralia, pelvis and part of sternum of *Crocodilus* (Voeltzkow und Döderlein, '01); cartilage stippled, bones l o u t l i n e d. *g*, gastralia; *i*, ischium; *p*, pubis; *r*, ribs; *s*, sternum.

Among Cetacea scales are known in *Neomeris, Phocæna* and *Globiocephalus* and in the fossil Zeuglodonts which had a more complete armor of bony plates. The plates of *Neomeris* are about 4 mm. across, and are arranged in somewhat regular rows on back and head, on the radial side of the appendages and on the dorsal fin. Their number and distribution are more restricted in the other genera.

Although closely connected with the skin, the horn cores (p. 195) of Ruminants (Bovidæ, Cervidæ, etc.) are developments of the periosteum of the frontal bones (sometimes of the parietals as well) and are not parts of the dermal skeleton.

ENDOSKELETON

The endoskeleton is outlined in cartilage, but membrane bones may be added to the primitive framework, especially in the heads of the higher groups. In Cyclostomes and Elasmobranchs it never passes beyond the cartilage stage, but in all other groups more or less of the cartilage is converted into bone, the amount of this increasing, the higher the animal in the scale. To the cartilage bone thus formed, membrane bones are added, these being most numerous in the skull, there being none in vertebral column or ribs and few in the appendicular skeleton.

AXIAL SKELETON

This includes the framework of head, trunk and tail, together with a larval structure, the notochord or **chorda dorsalis** which persists largely or wholly in the lower Vertebrates. Skull and vertebral column enclose and protect the central nervous system, the skull, from this standpoint being an enlarged anterior part of the vertebral column; but it must be remembered that Oken's "Vertebral Theory of the Skull" was overthrown years ago. The skull also surrounds a part of the digestive tract and thus a part of it is concerned in taking food. It also embraces organs of special sense which have modified it. The vertebral column, made up of separate metameric elements, the **vertebræ,** gives strength to the body and serves for the attachment of trunk and caudal muscles, while the ribs and sternum, when present, enclose the greater part of the viscera. Vertebræ, sternum and ribs either persist as cartilage through life, or, preformed in cartilage, ossify later to varying extents. The skull has a cartilage framework, the **chondrocranium,** most of which (Cyclostomes,

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Elasmobranchs and Chondrostei excepted) is transformed into or covered by bone long before the adult stage is reached. The part of the skull surrounding the alimentary tract—the **visceral skeleton** —is also laid down in cartilage. Both chondrocranium and visceral skeleton are reinforced by numerous membrane bones, most of which are shown by comparative anatomy to be derived directly from the skin and are comparable to the dermal skeleton just considered.

Vertebral Column

In its fullest development the vertebral column (**spina dorsalis** or 'backbone') consists of a series of metameric bodies, the verte-bræ, which alternate with the muscle segments and are usually some-what moveably articulated with each other, so that the column is flexible. Each vertebra surrounds the notochord and spinal cord,

and in the tail, the caudal blood vessels as well. In the lower Vertebrates each vertebra consists of little more than its portion of the chorda and the arches surrounding the spinal cord and blood vessels. In the higher groups these parts may fuse, the notochord may be lost and the whole may ossify in the adult. For convenience of reference a typical vertebra is described first.

Each typical vertebra (fig. 15) consists of a **body** or **centrum,** developed around the notochord, and bearing two arches, a **neural arch** above, surrounding the spinal cord; a similar **hæmal arch** on the ventral side, around the ventral blood vessels. Each arch consists of a pair of plates (**neurapo-physes** above, **hæmapophyses** below), each arch being completed by a keystone, the **neural** or **hæmal spine** (**spinous processes**). In the trunk the hæmal arch is modified or absent.
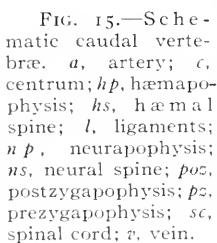
FIG. 15.—Sche-matic caudal verte-bræ. *a*, artery; *c*, centrum; *hp*, hæmapo-physis; *hs*, h æ m a l spine; *l*, ligaments; *n p*, neurapophysis; *ns*, neural spine; *poz*, postzygapophysis; *pz*, prezygapophysis; *sc*, spinal cord; *v*, vein.

Other parts may be connected with these. There are usually **pre-** and **post-zygapophyses** (**articular processes** of human anatomy) on the anterior and posterior faces of the neurapophyses, which strengthen the articulation of the vertebræ. (There may be addi-tional zygapophyses on the hæmal arches of fishes.) The sides of the vertebra may have **'transverse processes'** for the attachment of muscles and the articulation of ribs. Of these transverse processes

there may be two on a side, a **diapophysis** on the neurapophysis and a **parapophysis** in the centrum. Neural and hæmal arches of successive vertebræ are connected by dorsal and ventral longitudinal ligaments (sometimes two dorsal) which run on the chordal side of the spinous processes.

A vertebra is complex in origin. Reference must be had to special papers for details; many points are uncertain, but an outline of the development is necessary to understand structures and homologies in many groups.

Vertebræ are formed around most of the notochord which extends from the posterior half of the skull to the tip of the tail, just beneath the spinal cord. The notochordal cells, at first distributed through the chorda, rise to its surface where they form an epithelial-like (**epitheliomorph**) **layer** (fig. 16) which, with its external limiting
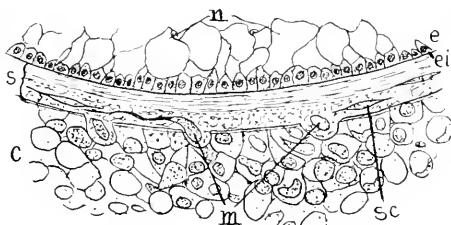

FIG. 16.—Formation of notochordal sheath in *Callorhynchus* (Schauinsland, '05). *c*, cartilage of sclerotome; *e*, epitheliomorph layer of *n*, notochord; *ei*, elastica interna; *m*, cartilage cells invading *s*, notochordal sheath; *sc*, cartilage cells in sheath.

membrane, is called the **elastica interna.** The epitheliomorph cells secrete a non-cellular envelope, the **notochordal sheath,** the external layer of which, the **elastica externa,** differs from the rest. Neither chorda or sheath show metamerism, except as later they are influenced by structures developed around them.

The myotomes (p. 2) lie laterally on either side, each with its myocœle, bounded by somatic and splanchnic walls. The dorsal part of the splanchnic wall (fig. 2) forms the voluntary muscles of the body, which, in lower Vertebrates, largely retain their metamerism through life. The more ventral part of this wall (in lower Vertebrates part of the mesothelium ventral to the myotomes may participate) forms mesenchyme, a part of which develops into the vertebra; hence these mesenchymatous bodies are called **sclerotomes.** The successive sclerotomes are limited by vertical blood vessels, and each sclerotome is at first divided vertically by a gap into cranial and

caudal halves (fig. 17, *A*), a matter of importance in tracing the history of the parts of a vertebra.
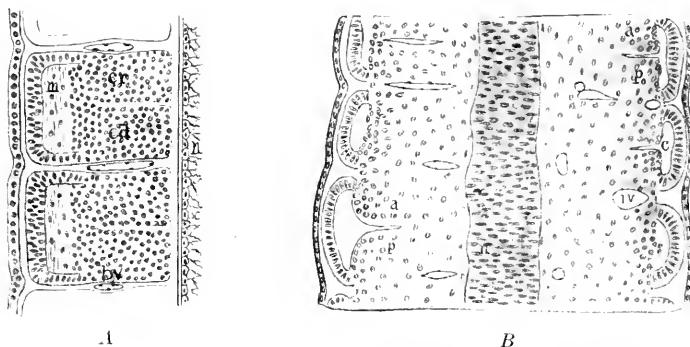

FIG. 17.—*A*, developing sclerotomes of *Sceloporus; B*, of *Tropidonotus* (Corning). *a*, cranial half-sclerotome; *c*, myocœle; *cd*, caudal half-sclerotome; *cr*, cranial half-sclerotome; *iv*, *bv*, intersegmental blood vessel; *m*, developing blood vessel; *n*, notochord; *p*, caudal half-sclerotome.

The medial portion of each sclerotome (cranial and caudal parts) migrates to the side of the notochord, its cells being largely aggregated in the V-shaped longitudinal grooves—dorsal and ventral—


FIG. 18.— Diagram of vertebrate embryo at beginning of mesenchyme formation showing grooves (*g*) between spinal cord (*s*), notochord (*n*), and artery and vein (*a* and *v*) where most scleroblasts accumulate. *m*, myotome; *ms*, mesenchyme budding from myotome.

between notochord and spinal cord above (fig. 18), and, in the tail between chorda and blood vessels. The dorsal of these cell masses on either side—two to a myotomic somite, corresponding to the half sclerotomes —extend upwards, tending to surround the spinal cord, while below, in the tail, the ventral cells enclose the caudal artery and vein in the same way. Later, chondrification of the parts thus formed results in the formation of neur- and hæmapophyses; not all of the mesenchyme cells are utilized in this, some form ordinary connective tissue.

Different names have been given to these eight vertebral elements, based either on their position or on a misconception of their fates. Although adding to an overburdened nomenclature, non-commital terms are suggested here. The two elements from the anterior half of each sclerotome are **cranineurals** and **cranihæmals** in the following account,
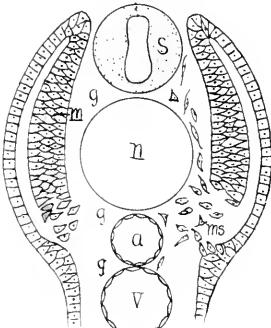
accordingly as they lie above or below the notochordal axis. Correspondingly **caudineurals** and **caudihæmals** arise from the posterior half sclerotome. Hence there are two pairs of neurals and two of hæmals—eight elements in all—to each original pair of myotomes.

The order of parts concerned in the development of a vertebra is: 1, intersegmental blood vessel (fig. 19); 2, ventral nerve root; 3, cranineural and crani-hæmal; 4, dorsal nerve root; 5, caudineural and caudihæmal; 6, intersegmental vessel. The interseg-mental vessels lie in the plane of the myosepta and alternate with the myotomes, thus affording a criterion of metameric limits.


FIG. 19.—Scheme of relations of half-scleroto-mes and their products to nerves and blood vessels in Elasmobranchs (based on Schauinsland). *c*, vertebral centra; *cd*, *cr*, caudal and cranial parts; *d*, *v*, dorsal and ventral nerve roots; *i*, intercentra; *b*, interseg-mental blood vessel.

The vertebræ arise from these various parts, but there is uncertainty in some cases as to the role played by each. There is one great difference between Elasmobranchs and higher Vertebrates; in the former cells from the sclerotomic elements just mentioned break through the elastica externa (fig. 16), invade the notochordal sheath, and may chondrify there. By extending in all directions these invading cells may meet above and below, forming cartilage rings around the notochord. In those higher Vertebrates where the history is known, cartilage cells do not invade the sheath, but surround the elastica, forming rings in that position. The sheath is greatly reduced in Amniotes and the two elasticæ are not differentiated.

In the tail of Cyclostomes (fig. 234) the neural elements extend up on the sides of the spinal cord, forming neurapophyses, their bases resting on the noto-chordal sheath, while hæmapophyses are formed in the same way on either side of the caudal blood vessels. There are no cartilages formed in the trunk of Myxinoids, but *Petromyzon* (fig. 83) has neurapophyses there. Since there are two half-sclerotomes to a myotome, there are two incomplete arches (no spinous process) to each original somite.

In Gnathostomes cranial and caudal elements develop unequally, the caudals being the larger and forming the greater part of the whole of the arches, the cranials being less developed. In lower Verte-brates (especially in some extinct Ganoids and Stegocephals) parts resulting from the chondrification of neurals and hæmals remain

separate (p. 37), but there is more or less fusion of parts, though in different ways, in most groups. It is stated that in some lower fishes (as Holocephali) cranial and caudal elements of the same original myotome unite to form a single vertebra, the cranial parts in front, the caudals behind, the vertebra being thus intrasegmental. In all others (fig. 20) the caudal parts of one somite unite with the cranials
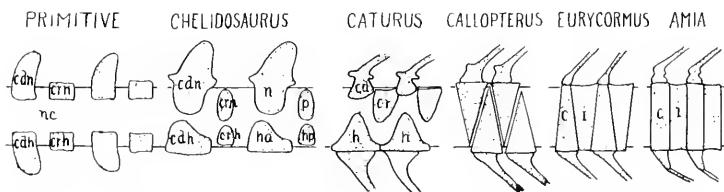

FIG. 20.—Scheme of vertebral elements in Stegocephal (*Chelidosaurus*) and Ganoid vertebræ. *c*, centrum; *cdh*, caudihæmal; *cdn*, caudineural; *crh*, cranihæmal; *crn*, cranineural; *ha*, hypocentrum arcale; *hp*, hypocentrum pleurale; *i*, intercentrum (intercalare); *n*, neurapophysis; *nc*, notochord; *p*, pleurapophysis.

of the next posterior to form the definitive vertebra which is thus intermyotomic, a condition more advantageous for the action of the trunk muscles. Details are given below.

The anterior and posterior faces of the centra may have different shapes in different groups. The most primitive has both faces excavate—**amphicœlous vertebræ** (fig. 21, *A*). In some fishes and many reptiles the centra are hollow in front and convex behind (fig. 21, *B*) the two vertebræ articulating by a ball and socket joint
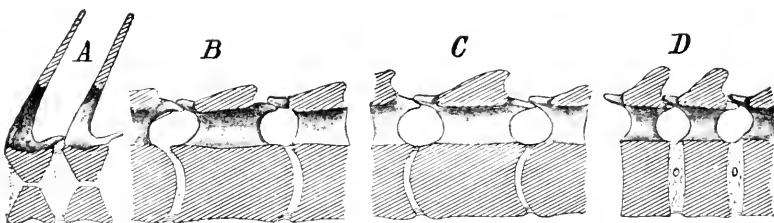

FIG. 21.—Sagittal sections of (*A*) amphicœlous, (*B*) procœlous, (*C*) opisthocœlous, and (*D*) amphiplatyan vertebræ; the left is anterior.

(**procœlous vertebræ**). In **opisthocœlous vertebræ** these conditions are reversed, the socket being on the posterior face (*C*). Most Mammalian vertebræ have the two faces flat (**amphiplatyan**) an **intervertebral disc** (**meniscus**) intervening between each two centra (*D*). An exception should be noted in the cervical region of Artiodactyls where most of the vertebræ are opisthocœlous.

RIBS

Ribs and their supporting structures are closely related to the vertebræ. In considering them it should be recalled that trunk and tail muscles are separated by a horizontal septum (p. 3) into epaxial and hypaxial series, the septum reaching the vertebral column at about the level of the centra. A second sheet of skeletogenous tissue, the median septum, lies on the medial side of these muscles—between them and the vertebræ in the tail, just outside of the peritoneum in the trunk. These two septa are intersected between the myotomes by the myosepta, and at any intersection skeletal parts may form.

In the caudal region of fishes the hæmapophyses are developed at the intersection of median and myosepta, and, with the hæmal spine, form arches which are usually closely connected with the vertebral centra and enclose the caudal artery and vein (fig. 22, A). Thus the hæmapophyses lie on the *medial* side of the caudal hypaxial muscles. In the trunk of fishes, besides the dorsal aorta, various viscera lie ventral to the vertebræ, some of them (alimentary canal,


FIG. 22.—Relations of muscles and the structures commonly called ribs. A, the condition in the tail of Urodeles; removal of the transverse processes would give the piscine condition; B, shows both kinds of ribs in the trunk; they coexist in but few forms. *ep*, epaxial muscles; *H*, hypaxial muscles; *h*, horizontal septum; *ha*, hæmal arch; *hr*, hæmal rib; *pr*, pleural rib; *t.* transverse process (true rib); *va*, vertebral artery.

gonads) liable to great variations in size at different times. Hence the closed hæmal arch of the tail is impossible here. But immediately beneath the peritoneum and at the intersection of myosepta and the scleroblastic tissue underlying the cœlomic lining (on the medial side of the hypaxial muscles) there are usually elongated skeletal elements, preformed in cartilage, resembling hæmapophyses in every respect, save that they are not connected ventrally by a hæmal spine (fig. 22, B. *hr*). They may be in actual continuity with the centra or may be articulated to a **'basal stump'** on the centrum. This condition permits changes in the size of the abdominal cavity. These rods are the 'ribs' of most fishes, which, from their evident homology with the hæmapophyses in the tail, are called **hæmal ribs.**

In a number of fishes (Crossopterygii, fig. 23, Salmonids, Clupeids) another type of ribs may occur along with the hæmal ribs. These lie in the intersection of myosepta and horizontal septum (fig. 22, *Bpr*) and hence between epaxial and hypaxial muscles. These are the **true** or **pleural ribs,** the only kind occurring in Tetrapoda.
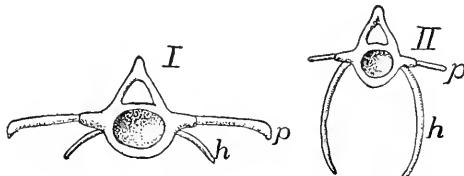

FIG. 23.—Vertebræ of anterior and posterior trunk regions of *Polypterus* (Gegenbaur). *h,* hæmal rib; *p,* pleural rib.

These pleural ribs occur in the tails of Urodeles (fig. 22, *A*) and many reptiles, attached (sometimes ankylosed) to the centra which also bear hæmal arches. In Urodeles these caudal ribs lie in the horizontal septum and are connected with the vertebræ by two heads, a dorsal connected with the neurapophysis, the ventral to the centrum, so that an opening (**vertebrarterial canal**) through which runs the vertebral artery, lies between centrum and rib.
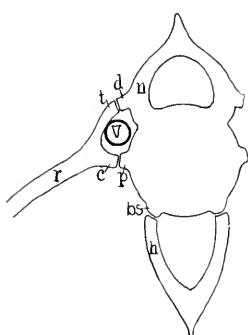
In the higher Vertebrates the same relations of the pleural ribs occur, except that in the anterior part of the trunk the hypaxial muscles are lacking, though often present further back ('tenderloin' of mammals). In Amniotes (fig. 24) the ribs are articulated with the vertebræ, usually by two heads, and with the same vertebrarterial canal as in the Urodele tail. The dorsal of these heads is the **tubercular head** of human anatomy, the ventral the **capitular head.** These articulate with processes from the vertebra, a dorsal diapophysis and a ventral parapophysis.

FIG. 24.—Schematic vertebra of Amniote. *bs,* basal stump; *c,* capitular head of rib; *d,* diapophysis; *h,* hæmal arch; *n,* neural arch; *p,* parapophysis; *r,* pleural rib; *t,* tubercular head of rib; *v,* vertebrarterial canal with vertebral artery.

In mammals, where the parapophysis is reduced, the diapophysis is called the transverse process and the same term is applied to the united diapophysis, parapophysis and rib in the cervical region of many forms. There is the same confusion of terms in the caudal region of some other Tetrapoda.

Another view of ribs is that they are homologous in all Vertebrata. In many there is a hæmal process (fig. 25) on the medial side of each hæmapophysis, extending between caudal artery and vein. Farther forwards, it is argued, the hæmapophysis divides, leaving the hæmal process attached to the centrum, the rest extending laterally as a transverse process. This gives the hæmal process a chance to expand as a hæmal rib, while a segmentation of the transverse process results in a pleural rib, explaining the presence of both kinds of ribs in the trunk of forms like *Polypterus* (fig. 23). It does not explain the closed arch and the pleural rib in the Urodele tail, nor how a sub-peritoneal rib can be the same as one in the horizontal septum.
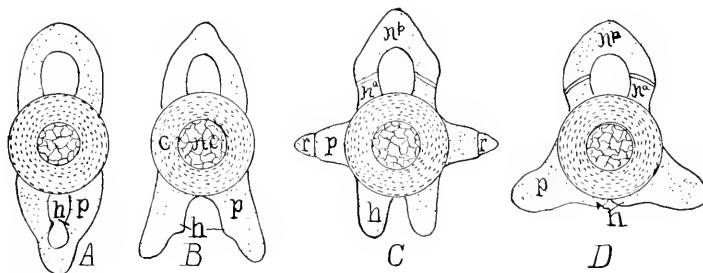

FIG. 25.—Schauinsland's homology of ribs, based on *Læmargus*. *A*, mid-caudal; *B*, base of tail; *C*, middle of trunk; *D*, cervical. *c*, centrum; *h*, hæmal processes; *na*, *np*, neural arch; *nc*, notochord; *p*, hæmapophysis; *r*, pleural rib.

Regions of the Vertebral Column.—The number of vertebræ in the column varies between wide limits and is correlated to some extent with the length of the animal. It is smallest in the Aglossate Anura where, not including the urostyle, there are eight (in other Anura nine) while some limbless lizards and some snakes have nearly five hundred. These vertebræ may be divided into groups or regions by important characters. Fishes have two such regions, **trunk,** where the vertebræ bear hæmal ribs, and **caudal** where the centra, at least anteriorly, support hæmal arches.

In Tetrapoda, except the limbless forms, the hind limbs are attached by their girdles to the vertebral column at a point between trunk and tail, the one or more vertebræ to which they are attached forming a **sacrum.** All recent Amphibia have but one sacral vertebra. Higher in the scale (most reptiles) a second vertebra is added to the sacrum, and, corresponding to the greater use of the hind limbs and an increase in body size, still other vertebræ may be included in the sacral region. The true sacral vertebræ are not articulated directly to the pelvis, a **sacral rib** intervening, which is usually fused with the sacrum, but retains its individuality in a few forms

(many Urodeles, fig. 280, Crocodilians, turtles, fig. 26, etc.). The sacral vertebræ may remain distinct or may fuse. Other vertebræ (**pseudosacrals**) frequently enter into pelvic relations, but these, lacking ribs, join the pelvis by their transverse processes. These
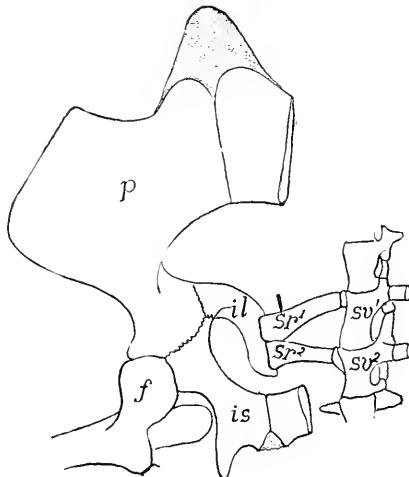

Fig. 26.—Sacral vertebræ, sacral ribs and pelvis of *Trionyx* obliquely from below. *f*, head of femur; *il*, ilium; *is*, ischium; *p*, pubis; *sr*, sacral ribs; *sv*, sacral vertebræ.

additions and the true sacrum make up a **synsacrum** which reaches its extreme in birds (the oblique position of the body necessitating a strong support), where the synsacrum may include twenty vertebræ,
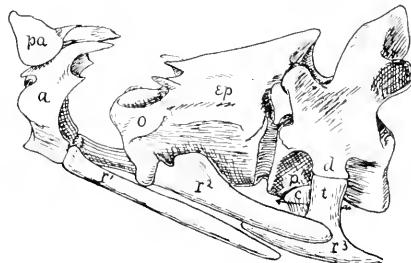

Fig. 27.—Three anterior vertebræ of *Rhamphostoma* (Crocodilian; Schimpkewitsch, '21). *a*, atlas; *c*, capitular head of rib; *d*, diapophysis; *ep*, epistropheus; *o*, odontoid process; *p*, parapophysis; *pa*, proatlas; *r*, cervical ribs, the arrow through the vertebrarterial canal; *t*, tubercular head of rib.

only two of which are true sacrals, the others being added from caudal and lumbar regions.

In Amphibia the presacral vertebræ, except the first (atlas), bear ribs, the atlas here is regarded as forming a **cervical** region, the

other trunk vertebræ making a **dorsal** region. In other Tetrapoda the number of cervical vertebræ varies extremely. These are characterized by the entire absence of ribs or by extremely short ones, so reduced that they do not reach the sternum. Again, not all post-cervical vertebræ may bear ribs; those which bear ribs form a **thoracic** region, those without ribs a **lumbar** region.

Two of the vertebræ have received special names, the first, to which the skull is attached, is the **atlas.** In most Tetrapoda this is followed by the **epistropheus (axis)** which has not only its own centrum, but that of the atlas has joined that of the epistropheus, forming a pivot (**dens epistrophei, odontoid process**) on which the atlas, and with it the head, turns. In a few reptiles and *Erinaceus* (mammal) a bone, apparently a neural arch which has lost its centrum, occurs between the atlas and skull (fig. 27). This is the **proatlas,** the morphology of which is uncertain. As it is preformed in cartilage it cannot be regarded as other than vertebral.

CYCLOSTOMATA have a persistent notochord, but other parts of the vertebral column are poorly developed and no ribs occur. There are some minor differences between the two orders. In the trunk region of *Petromyzon* (fig. 83) there are two pairs of neurapophyses to a somite, lying in the connective tissue which surrounds the axial structures. They do not meet above the spinal cord, the arches being incomplete. In the caudal region the same parts fuse to a continuous plate of cartilage, with foramina for the exit of the spinal nerves, which bears processes, usually regarded as dorsal spines. Near the end of the tail in the hæmapophyses form a similar plate with hæmal spines. In Myxinoids (fig. 234) no arches or neurapophyses are developed except in the tail where both neur- and hæmapophyses occur, fused into dorsal and ventral plates, *Myxine* remaining in this respect on a level with the larval (*Ammocœtes*) stage of *Petromyzon*.

A small fossil, *Palœospondylus*, from the Scottish Devonian may be mentioned here. Its systematic position is most uncertain. The skull, absence of paired fins, a diphycercal tail and a caudal fin supported by delicate, often branched, fin rays, have led some to regard it as near the Cyclostomes. But against this may be mentioned the perfect vertebral centra (unknown in any Cyclostome) and the difficulty of comparing the skull with that of recent Cyclostomes. It is also suggested that it is a larval Dipnoan, but this does not account for the centra. The vertebral column is long and slender, consisting of numerous centra, each with its neutral arch, while both neural and hæmal arches occur in the tail. The vertebræ seem to be more distinct in front.

PISCES.—The vertebral column differs greatly in different fishes, but some general statements may be made. It is most primitive

in the lower Elasmobranchs, Chondrostei (fig. 28) and Dipnoi which
resemble Cyclostomes in having only arches and no centra.   In
other fishes centra are formed by the bases of hæmals and neurals
around the notochord.   As a rule only the caudineurals develop
neurapophyses, and in the tail the caudihæmals form hæmapophyses,
while the cranial half sclerotomes usually do not form such out-
growths.   As a result many fishes have two or more rings, more or
less complete, to each myotomic somite.   The ring with arches is
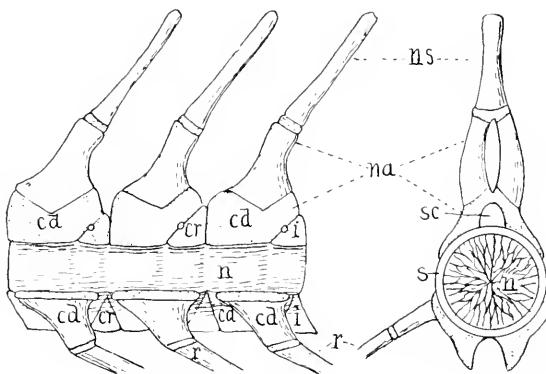
FIG. 28.—Vertebræ of *Acipenser* (R. Hertwig, '91).   *cd*, caudihæmals and -neurals;
cr, cranihæmals and -neurals; (*i*, intercalaria); *n*, notochord; *na*, neural arch; *ns*, neural
spine; *r*, ribs; *s*, notochordal sheath; *sc*, spinal canal.

called the centrum, the one without is an **intercentrum** or **intercalare**
(fig. 20), but, as will appear later, the two together are the equivalent
of the centrum of Tetrapoda.

This double condition of centra is called **diplospondyly**.   Sometimes a whole
myotome and the corresponding nerves have apparently been lost, while the
vertebral parts have been retained, **polyspondyly** resulting.   In the higher
Ganoids and in Teleosts centrum and intercentrum unite to form a single (true)
centrum, a condition found in most Amniotes.   Except in a very few cases the
caudal half of one primitive sclerotomic segment fuses with the cranial half
of the next posterior, the result being an alternation of centra and vertebræ with
muscular segments (p. 22).

In the trunk there are no complete hæmal arches, the hæma-
pophyses being, as explained above, hæmal ribs, but in some fishes
parts of the hæmapophyses form a reduced hæmal arch around the
dorsal aorta, as in Chondrostei where the hæmal ribs are greatly
reduced or absent.   Usually the basal stumps lie higher on the sides

of the centra farther forwards and may be borne anteriorly even at the level of the neural arch.

The vertebræ are never ossified in Elasmobranchs, but may be calcified (p. 6). In Chondrostei bone may be deposited on the outside of the cartilage; and every stage may be traced from this to conditions in which practically all of the cartilage of the vertebra is replaced by bone.

ELASMOBRANCHII have considerable variety in vertebræ. Possibly the most primitive is found in the extinct Xenacanthidæ (fig. 29) where several elements (but no centra) appear to each somite, these being apparently comparable to the parts in the better known cartilaginous Ganoids and referable to the neurals and hæmals of the developmental stages of other Elasmobranchs (p. 19).
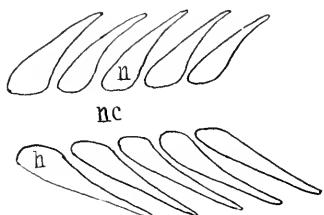

FIG. 29.   FIG. 30.

FIG. 29.—Five caudal vertebræ of *Xenacanthus* (Fritsch). *h*, hæmal arches; *n*, neural arches; *nc*, position of notochord.

FIG. 30.—Vertebræ of *Chimæra* (Schauinsland). *cdn*, *crn*, caudi- and cranineurals; *dr*, dorsal roots of spinal nerves; *h*, hæmals; *n*, notochord with calcifications; *vr*, ventral roots of spinal nerves.
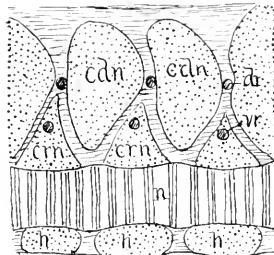
Of living Elasmobranchs the Holocephali, so far as vertebræ are concerned, are the most primitive (fig. 30), while Notidanids, *Echinorhinus* and *Læmargus* are scarcely more advanced. Holocephals develop the eight parts described above to a somite. In the trunk only the caudineurals form neurapophyses, the cranials (intercalaria) remaining small, their bases resting on the notochordal sheath, the upper margin rising but slightly on the side of the spinal cord. Each cranineural grows around a ventral root of a spinal nerve, the dorsal root passing out between the successive neurapophyses (fig. 30). Fusion of hæmals forms a plate on the ventral side of the notochord. At first the neurapophyses do not meet above the spinal cord, but do later, and the gaps between the succes-

sive neurapophyses are closed by **roof plates,** possibly modified spin-
ous processes. As neurals and hæmals do not meet on the sides of
the notochord, no centra are formed, but there are non-metameric
calcifications of the chordal sheath in *Chimæra*. In the adult the
various parts fuse with little regularity, while just behind the head
a large number of vertebral segments unite so that the centra are
composed of a cranial half followed by a caudal half, each entirely
enclosing the notochord.

In more normal Elasmobranchs centra arise by chondrification
within the sheath (p. 19), these corresponding rather closely to the
neurals and hæmals of the early stage and situate at about the level
of the myosepta. These centra restrict the chorda, which therefore
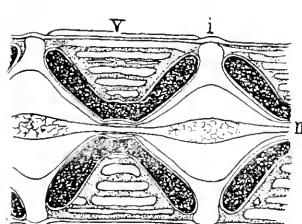
FIG. 31.
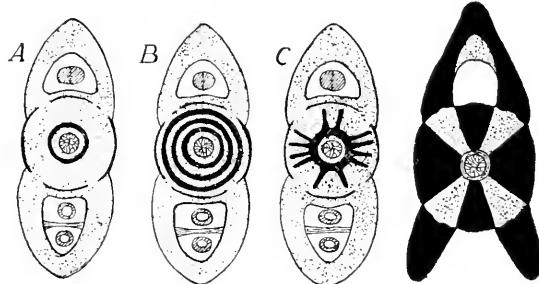
FIG. 32.   *D*

FIG. 31.—Longitudinal section of vertebræ of *Squalina* (Hasse, '79–82). *i.* inter-
vertebral line; *n*, notochord; *v*, vertebral centra; heavily calcified parts of amphicœlous
centra darkest, around these (stippled) are rings of calcified cartilage. Unmodified
notochordal tissue light.

FIG. 32.—Diagrammatic sections of vertebræ. *A*, *B*, cyclospondylous Elasmo-
branchs; *C*, asterospondylous Elasmobranch; *D*, cross section of Teleost vertebra; bone
black, cartilage stippled.

can increase in diameter only at the level of the middle of the parent
myotomes. Thus the notochord becomes a series of intervertebral
enlargements and vertebral constrictions, and, as the centra increase
in length, they adapt themselves to this condition, extending
over the intervertebral enlargements, thus becoming shaped like
an hour-glass, hollow at either end (amphicœlous, fig. 31). The
successive centra are connected by the ligamentous parts of the
sheath in which no cartilage is ever developed. Later, the centra
increase in thickness and the successive layers of cartilage are calci-
fied. In some sharks these layers form complete rings so that a
transverse section shows concentric layers of hard and softer parts
(**cyclospondylous vertebræ,** fig. 32, *A*, *B*). In others no calcifica-

tion occurs under the bases of the arches (and in some other places) and then sections show radiations of calcified cartilage (**astero-spondylous vertebræ,** fig. 32, *D*). *Cetorhinus* has both radial and concentric calcifications.

Both neural elements, cranial and caudal, extend partly or entirely around the spinal cord, but develop to varying extents in different genera. The caudineurals form the neurapophyses, the ventral nerve roots passing through them or between them and the following cranineurals. Usually the cranineurals (intercalaria) do not extend dorsally as far as do the caudineurals, but may meet above the spinal cord, closing in the spinal canal (fig. 33), but as a rule their upper ends remain at a lower level, while a roof-plate
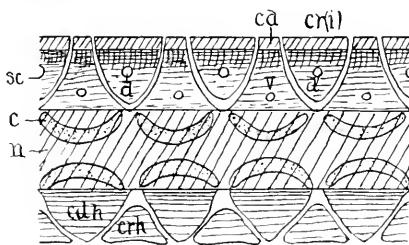

FIG. 33.   FIG. 34.

FIG. 33.—Sagittal section of *Acanthias* vertebræ, cut surfaces lined obliquely. *c*, calcifications of centra; *cd*, caudineurals; *cdh*, caudihæmals; *cr* (*i*), cranineurals (intercalaria); *crh*, cranihæmals; *n*, notochord; *sc*, spinal canal.
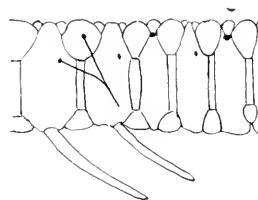
FIG. 34.—Vertebræ of *Heterodontus* at junction of trunk and tail (Daniel, '15).

covers the spinal cord in the intervals between the neurapophyses. The dorsal nerve roots are usually enclosed in the intercalaria.

The hæmal arches are usually complete in the anterior caudal region, but intercalaria are rare, and the hæmapophyses are but slight projections from the centra, either side of the dorsal aorta, and in front they may rise to the level of the neurapophyses. Diplo-spondyly and even polyspondyly often occur in the tail, there being two or more sets of vertebral elements to a pair of muscles and spinal nerves. Some evidence suggests that this is due to the obliteration, in phylogeny, of nerve and muscle segments, the vertebræ remaining.

Fusion of vertebræ is frequent at the anterior end of the column, especially in skates where fused segments afford support to the pectoral girdle. In sharks the column is firmly attached to the skull, but in skates and Holocephals an articulation occurs between them.

Most Elasmobranchs have short ribs articulated to the vertebræ (fig. 34), and as these are in the horizontal septum, they are pleural ribs, the homologues of those of Tetrapoda. In a few species there are similar ribs in the tail along with normal hæmal arches. Ribs are lacking in Chimæroids and many skates.

GANOIDEI show a wide range of vertebral structure. The Chondrostei (fig. 35) about parallel the Holocephali, having two sets of neurals and hæmals to a somite, these resting upon the thick

Fig. 35.—Developing vertebræ of *Polyodon* (Schauinsland, '05). *cdh*, caudihæmal; *crh*, cranihæmal; *crn*, cranineural; *dr*, dorsal nerve root; *n*, notochord; *ns*, neural spine; *v*, intersegmental blood vessel; *vr*, ventral nerve root.

fibrous sheath of the notochord, but not forming centra, the vertebræ consisting merely of chordal sheath and neur- and hæmapophyses. The caudal elements are best developed, forming in the tail, both apophyses; in the trunk the cranial parts form intercalaria; the caudal, neurapophyses. The hæmal arch is complete with hæmal spine in the tail, and a hæmal process (p. 25) may extend between caudal artery and vein. In the trunk the hæmapophyses are remote from each other and are divided into basal stumps and hæmal ribs lying just beneath the peritoneum. The cartilage column of sturgeons (fig. 28) may have superficial ossifications on parts of the arches. Anteriorly several vertebræ may fuse into a tube around the notochord, and in turn, be fused with the cranium.

Some fossil Ganoids show conditions leading to the bony Ganoids of today, but some uncertainty exists as to the interpretation of parts, as only the bones are preserved and there are no indications of what cartilages existed. In some there was the same condition (Cope's **rhachitomous vertebræ**) as in living Chondrostei. Others, like *Callopterus* (fig. 20) had an unequal development of cranials and caudals, these extending on the sides of the notochord so that in side view it was entirely enclosed, neural and hæmal elements alternating as a series of wedge-shaped bones (**embolomerous vertebræ**). A greater development of the cranial elements would result in centra and intercentra like those of modern *Amia*.

The bony Ganoids (Crossopterygii and Holostei) have extensive ossifications and distinct centra, these last, in larval *Amia*, being like those of the adult sturgeon. Later a superficial ossification—especially on the sides between neural and hæmal arches (fig. 20) results, in the tail, in two rings, centrum and intercentrum, to each myotome, the classical example of diplospondyly. In the trunk centrum and intercentrum fuse (sometimes three of these rings unite and the arch shifts to the intercalated ring). *Amia* and *Polypterus* have amphicœlous vertebræ; those of *Lepidosteus* (fig. 36) are opisthocœlous. This is caused by an extension inwards of intervertebral cartilage cutting off the notochord, then an incision cuts the cartilage in such a way that ball and socket result, the process resembling that occurring in Amphibian vertebræ (p. 38).
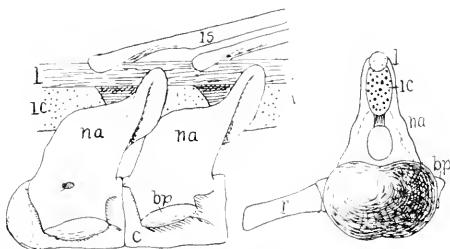
Fig. 36.—Lateral and anterior faces of *Lepidosteus* vertebræ (Balfour and Parker, '82). *bp*, basal process; *c*, centrum; *ic*, intercalary cartilage; *is*, interspinous bones; *l*, dorsal ligament; *na*, neural arch; *r*, hæmal rib.

Amia and *Lepidosteus* have hæmal ribs like those of Teleosts, but the existing Crossopterygians (*Polypterus* and *Calamoichthys*) have, in addition, pleural ribs articulated to parapophyses and extending almost horizontally between ep- and hypaxial muscles (fig. 23).

TELEOSTEI.—The vertebræ of Teleosts develop much like those of Holostei, caudal and cranial parts of two successive somites fusing to a single centrum, which, with few exceptions, is amphicœlous, enlargements of the notochord persisting in the cavities in the centra, the cavities often connected by a **dicentral canal** filled with the constricted chorda. In the early stages the parts are much as in the lower fishes, and ossification starts from these and extends to the centra. Frequently no ossification occurs beneath the arches, the result (fig. 32, *D*) being very like the asterospondylous centra of Elasmobranchs. Successive layers are added to the bone first formed, these coming from the perichordal tissue without the intervention of cartilage. Dorsal to the spinal cord there may be, as

3

in *Lepidosteus*, intercalated cartilages, but differing from the intercalaria of other groups.

The neural arches of the adult (separated from the centra in a few forms) are closed by neural spines, and the same holds for the hæmal arches in the tail. There is usually a regular transition from the caudal hæmal arches to the hæmal ribs of the trunk, these latter lying just beneath the peritoneum and being usually articulated to basal stumps, the latter placed higher on the sides of the centra further forwards, even on the neurapophyses near the head. The form and length of the hæmal ribs varies considerably, even in the same fish. In some Pleuronectids complete hæmal arches occur on the ventral side of the trunk vertebræ, no hæmal ribs being present. Lophobranchs and Plectognaths lack both kinds of ribs.

FIG. 37.—Bones of anterior caudal region of *Alosa* (Bütschli, '10). *c*, vertebral centrum; *h*, hæmal base; *hr*, hæmal rib; *i*, hypomeral; *m*, epicentral; *s*, epineural.

The neural arches bear pre- and postzygapophyses, and in the tail similar interlocking structures may occur on the hæmal arches. These make the column more firm and the whole is strengthened by longitudinal ligaments between the zygapophyses. In some Scombrids the zygapophyses of the two sides meet dorsal to the spinal cord, adding to the roof of the spinal canal. Dry skeletons frequently show two canals in the neural arch, the normal spinal canal, and dorsal to this, one for the longitudinal ligament (p. 19).

The number of vertebræ in Teleosts is variable, the larger number occurring in the eel-like fishes, while some Teleosts may have as few as twenty-three in the trunk. Very commonly the anterior vertebræ are fused, and the resulting bone may fuse with the cranium, or the connexion between column and skull may be strengthened by the spinous process of the first vertebra.

Besides the hæmal ribs, some fishes like the shad and herring have numerous slender bones of membrane origin among the trunk muscles in the myosepta and horizontal septum. They have no common name, but are grouped according to position (fig. 37) as **epimerals, epicentrals** and **hypomerals.** They are frequently forked, one branch coming into close relations with the vertebral column.
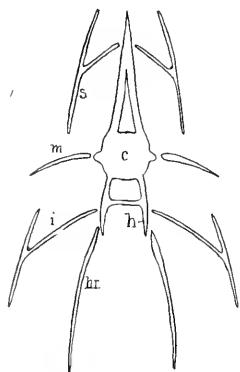
DIPNOI.—Although higher than the Teleosts in several respects, the lung fishes have a very primitive vertebral column, standing in this respect on a level with the Holocephali. Distinct centra are lacking, except at the anterior end of the column where two or three neurals and hæmals may unite in a ring around the notochord. Elsewhere the neural arches rest on the partly calcified notochordal sheath (fig. 38), meet above the longitudinal ligament, and are continued dorsally by long spinous processes, which may be jointed
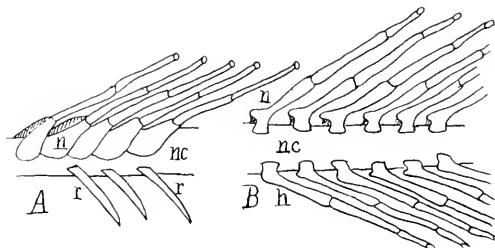
Fig. 38.—Vertebræ of *Lepidosiren* (Bischoff, '40). *A*, just behind head; *B*, middle of tail; *h*, hæmal arches; *n*, neural arches; *nc*, notochord; *r*, ribs.

·and usually are the supports of the dorsal fin. The caudal hæmal arches are much like the neural and usually have spinous processes. Intercentra occur only in the tail, caudal to the neural arches (apparently cranial elements) these being rudimentary in *Protopterus*. The centra are larger in the posterior caudal region of *Ceratodus*, and near the tip of the tail (fig. 39) is a series of centra-like bodies with ossi-
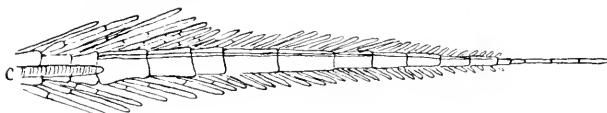
Fig. 39.—End of vertebral column of *Ceratodus* (Günther, '71). *c*, end of notochord.

fied neural and hæmal spines. The anterior of these centra contain notochordal tissue, but farther forwards this is replaced by cartilage. The vertebræ are cartilage, but may have a strong external layer of bone. There are hæmal ribs in the trunk which are continuous with the hæmal cartilages on the notochord, the anterior of these being peculiar in being separate from the column and attached to the cranium (the so-called head rib, fig. 122).

TETRAPODA.—In Tetrapoda the notochord is relatively smaller than in fishes, being best developed in Amphibia (fig. 43), where both elasticæ are present, although the tissue between them is

slight and the whole sheath very thin. The chorda is still smaller in Amniotes and its sheath is a single layer, apparently the elastica externa. In existing Tetrapoda the vertebræ are usually better ossified than in most fishes. Neural arches are well developed, and in the tails of the lower forms, the hæmals as well, but in the higher Amniotes the hæmal arches (**chevron bones**) are small or are entirely absent. A few Tetrapods have distinct intercentra in the trunk.

There are always zygapophyses in the trunk region and there may be (reptiles, p. 43) additional means of strengthening the articulation of the vertebræ. All Tetrapoda, except those lacking hind limbs or with them rudimentary, have a sacrum. Hæmal ribs never occur, but all have pleural ribs on some or all of the trunk vertebræ.

AMPHIBIA have, at most, four vertebral regions —cervical (one vertebra), dorsal, sacral and caudal. Gymnophiona and Aistopodous Stegocephals, which lack limbs, lack a sacrum and the Cæcilians have no caudal vertebræ. The caudals of Anura (fig. 40) are fused to a single bone, the **urostyle** or **coccyx**. Most Anura have eight presacral vertebræ, one sacral and the urostyle, the number of vertebræ entering the latter being unknown, this structure developing during metamorphosis. Gymnophiona may have 275 verte-bræ. The vertebræ are relatively short in Anura, longer in the other orders. Each bears a diapophysis which supports the rib which is usually very short, sometimes a mere particle on the end of the diapophysis.

FIG. 40.—Vertebral column of *Discoglossus* (Wiedersheim, '86). *a*, atlas; *r*, ribs; *s*, sacrum; *u*, urostyle.

The vertebræ are most primitive in STEGOCEPHALA, some of which resemble the Chondrostei, some are more like Holostei, others are peculiar in vertebral structure. The most primitive had a persistent notochord with elements on the sides of the sheath, apparently homologous with those of sturgeons (p. 32). One group of ossicles, apparently belonging to the caudal half sclerotome, consisted of a pair of neurals, bearing zygapophyses (fig. 42, *B*) and forming a neural arch. In the transverse plane with these and on the ventral side of the chorda are a pair of caudihæmals, usually united below to a single plate, called the **hypocentrum arcale**. The

cranial elements of the next somite are a pair of cranineurals (**pleurocentra**) and a corresponding pair of cranihæmals (**hypocentra pleuralia**), the whole forming a **rhachitomous** vertebra (p. 32).

In other Stegocephals there was apparently a fusion of the caudal parts with each other, and a similar union of the cranials, resulting in an **embolomerous** condition (fig. 42, *D*) with centra and inter-
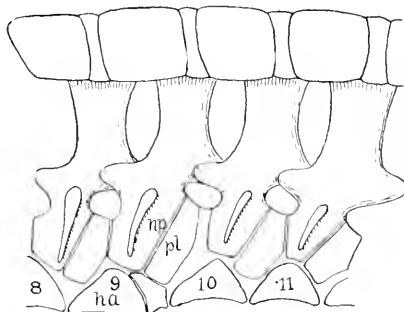

FIG. 41.—Trunk vertebræ of *Cacops* (Williston, '10).   *ha*, hæmals; *np*, neurapophysis; *pl*, pleurapophysis.

centra as in *Amia*. Other modifications give other shapes. In the highest Stegocephals, as shown in the larvæ of *Mastodonsaurus*, centra and intercentra have fused, forming true amphicœlous vertebræ, the notochord continuing through the dicentral canal. Other
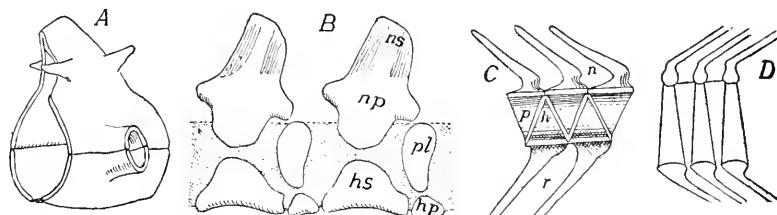
FIG. 42.—Stegocephalian and genoid vertebræ (Zittel, Woodward). *A*, phyllospondylus; *B*, rachitomous (*Chelydosaurus*); *C*, *Callopterus*; *D*, embolomerus (*Eurycormus*). *hs*, hypocentrum arcale; *hp*, hypocentrum pleurale; *np*, neurapophysis; *ns*, neural spine.

genera apparently have lost the cranial parts, the vertebræ being formed entirely by the caudal half sclerotome.

Two more types of centra occur in Stegocephals. The **lepospondylous** type is a ring of skeletal material restricting the notochord intervertebrally, allowing it to expand between the centra. Increase in length of the ring, as in Urodeles, results in amphicœly. In

phyllospondylous vertebræ (fig. 42, A) neural and hæmal parts have joined, but the hæmals do not meet beneath the notochord, the result being an imperfect centrum with no evident pleurocentra. In both these types the bone apparently formed a thin layer on the outside of cartilage which has left no trace. Stegocephals had long, well-developed ribs, frequently bicipital and bearing uncinate processes, like those of birds, which strengthened the skeletal basket.

URODELA have the cartilage elements laid down early, both cranial and caudal parts occurring, the former soon disappearing as discrete parts (pleurocentra or intercalaria). The hæmals are small in the
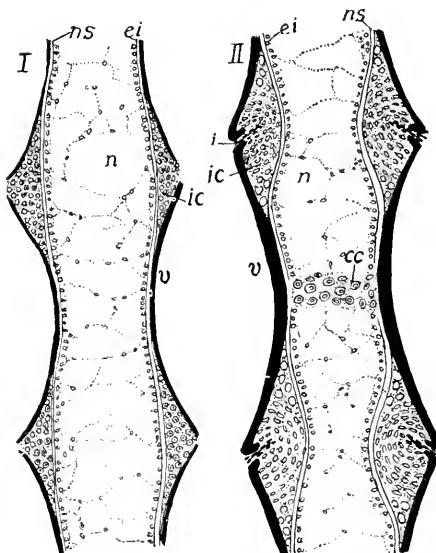
FIG. 43.—Two stages in development of vertebræ of *Amblystoma*. *cc*, cartilage in centre of vertebra; *ei*, elastica interna; *i*, incisure cutting *ic*, intercentral cartilage; *n*, notochord; *v*, vertebra (bone) black.

trunk. Ossification begins early around the cartilages and noto-chordal sheath, much as in Teleosts, resulting in an elongate biconical ring of bone (fig. 43). Between each two of these rings (*i.e.* inter-vertebrally) the cartilage increases, extends inwards, constricting and eventually obliterating the notochord here. From these points cartilage gradually grows forwards and backwards, between bone and sheath, to the middle of the centrum where the notochord itself may chondrify. This intervertebral cartilage persists unmodified in Perennibranchs where no true joint forms between the amphicœlous vertebræ. In most Salamandrina the intervertebral cartilage is

larger, dividing, with growth in the same way as in *Lepidosteus* resulting in a ball and socket joint (opisthocœlous, fig. 43, *II*, *i*). A few Salamandrina are amphicœlous.

The Urodeles have low spinous processes and the trunk vertebræ have diapophyses. The hæmal arches in the tail are usually well formed, at least anteriorly. The first vertebra (atlas) has its centrum greatly reduced, and on either side has a cup-shaped depression for the occipital condyle of the skull.
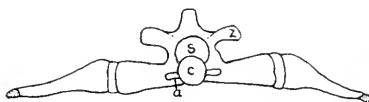
FIG. 44.—Vertebra of adult *Cryptobranchus japonicus* (Hoffmann, '74). *a*, vertebrarterial canal; *s*, spinal canal; *z*, zygapophysis.

The Urodele rib has apparently been misunderstood. The relations in the tail are normal (fig. 22, *A*) except that the rib, between ep- and hypaxial muscles, is continuous with the centrum. In the trunk of a three months larva of *Cryptobranchus* (fig. 45, *A*) the same parts are recognizable, but later, as in *Triton*, the part representing
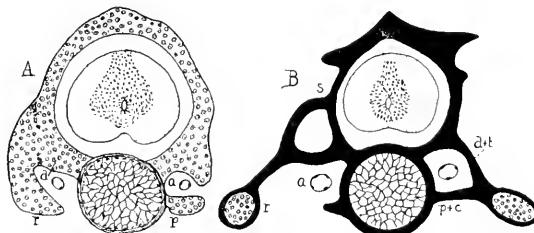
FIG. 45.—*A*, Vertebra of *Cryptobranchus alleghaniensis* 3 months after hatching; *B*, *Triton* 35 mm. long, right and left sides from different sections. *a*, vertebral artery; *d* + *t*, diapophysis and tubercular head; *p*, parapophysis; *p* + *c*, parapophysis and tubercular head; *r*, rib; *s*, secondary connexion of rib and neural arch.

diapophysis and tubercular head has been perforated (fig. 45, *B*) so that there is a secondary connexion (*s*) of rib and vertebra, while ventrally the parapophysial-capitular connexion has largely disappeared. In some genera the rib extends farther and becomes segmented in such a way as to appear as if the upper connexion were the tubercular one and the true tubercular looks like a capitular. It is clear from the earlier relations that the Amphibian rib is homologous with those of Amniotes.

The vertebræ of GYMNOPHIONA (fig. 46) are much like those of Perenni-branchs in having no division of the intervertebral cartilage. They are relatively

FIG. 46.—Vertebræ of *Siphonops* (Wieder s h e i m, '79).

long, very numerous and each has a pair of transverse processes on either side, the ventral side bearing a spine directed forwards (probably united hæmapophyses), between the parapophyses. giving additional strength to the column. No caudal vertebræ occur. The short ribs are articulated to the transverse processes and terminate differently in the various genera.

ANURA (figs. 40, 47) are characterized by the small number and shortness of the vertebræ, recent species, with few exceptions, having eight presacrals and one sacral vertebræ, and a urostyle representing the fused caudals, while the atlas is the sole cervical.

In development the cartilages fuse early to a continuum in which no intercentral parts are recognizable. An intervertebral cartilage is formed between each two centra, dividing so that the ball and socket joint is usually procœlous, although a few genera (*Pipa, Bombinator*, etc.) are opisthocœlous. Exceptionally, in the same individual some centra are procœlous, some amphicœlous, and some biconvex. Usually in all, the eighth vertebra is amphicœlous, the sacrum having a ball in front. In some Anura (*Pelobates, Bombinator*) the vertebræ arise wholly from the neural elements, the hæmal being greatly reduced or lacking, so that the centra are epi- rather than perichordal.

FIG. 47.—Vertebral column of *Pipa* (H o ff m a n n, '7 4). *s*, sacrum; *u*, urostyle.

The atlas, lacking transverse processes, bears a pair of glenoid cavities, as in Urodeles, for articulation with the occipital condyles of the cranium. The diapophyses of the other vertebræ are large, longest on the sacrum where they articulate with the iliac bone. The sacrum has two posterior tubercles for articulation with the urostyle which is an elongate bone into which the spinal cord extends for a short distance, giving off a pair of coccygeal nerves which pass out through foramina in the sides of the bone. Coccyx and sacrum are fused in Aglossa (fig. 47), and in *Discoglossus* (fig. 40) the urostyle

bears a pair of transverse processes. The ribs of frogs and toads are always short, and it is a question whether the cartilages on the tips of the diapophyses of *Rana*, etc., are ribs or epiphyses.

AMNIOTA.—The frequent occurrence of amphicœlous vertebræ in reptiles, birds and mammals, at least in development, points to the origin of the group from an amphicœlous ancestor, but there are many points of vertebral ontogeny on which definite knowledge is lacking, as are also detailed comparisons with the neural and hæmal parts of Ichthyopsida. It is evident, however, that many genera have the same cranial and caudal half-sclerotomes (figs. 17, 48), and

that these play the same parts in forming a vertebra with caudal elements in front, cranial from the next following somite, behind.

The notochord is very small, its sheath greatly reduced, consisting of a single elastica, except in *Sphenodon* embryos where there is a thin interna and a slightly thicker externa. Until the appearance of skeletogenous tissue the diameter of the notochord is the same throughout, although it may have an undulating course. The neuropophysial cartilages are usually first to appear, the hæmapophyses in the tail appearing at the same time in some forms. In the trunk **hypochordal bars,** extending beneath the chorda and up on either side, are formed in procartilage. These, apparently, are hæmal elements comparable to the hypocentra arcalia of some Ichthyopsida (p. 36). With chondrification these bars join cartilages from the neural elements, forming rings around the notochord. In a few lizards intercentra arise between the successive neural arches, uniting soon with the principal parts.

FIG. 48.—Early stages in development of cervical vertebræ of cow (Froriep, '86). *A,* transverse of embryo 8.8 mm. body length; *B,* sagittal through basal plate and cervicals 1 and 2 of 25 mm. embryo. *c,* centra of atlas and epistropheus; *b,* basal plate of cranium; *g,* spinal ganglion; *h,* hypochordal bar; *m⁵,* fifth myotome; *n,* notochord.

The succeeding stages differ somewhat in Sauropsida and mammals. In *Sphenodon* and geckoes (which lack close vertebral articulation) the notochord persists between the centra, and the vertebræ are amphicœlous, as in several

fossil reptiles. In other Sauropsida where the development is known, inter-vertebral cartilage like that in Amphibia, occurs, interrupting the notochord in the same way, and then these are cut, partially or completely, and in such a manner that either pro- or opisthocœlous centra result, the notochord persisting for a time in the centra. In mammals, where development is imperfectly known, the chorda disappears, first, in the centra, but may persist through life in the fibro-cartilage discs (**menisci**) which separate the successive centra.

Hæmal ribs are not known in Amniotes, except as their homo-logues, the chevron bones persist in the tail.   Pleural ribs, either bicipital or with a single head, are always present, attached to the thoracic vertebræ and to more or fewer of the cervicals, while in the sacral region sacral ribs connect the vertebræ with the ilium of the pelvis.   When a sternum is present, the anterior thoracic ribs are connected directly with it, while those farther back are connected with those in front or end freely.

REPTILIA.—All types of vertebræ—amphi-, pro-, opisthocœlous and amphiplatyan—occur in reptiles, but usually one kind prevails
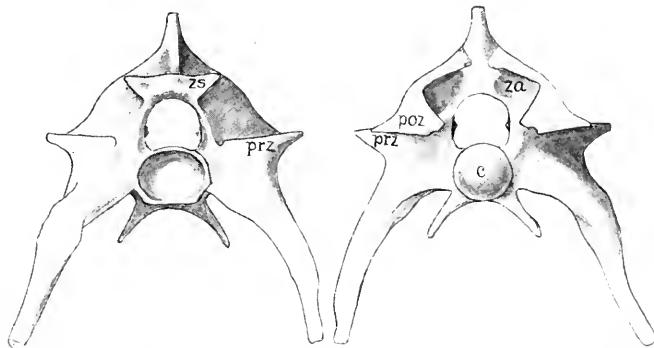
FIG. 49.—Anterior and posterior faces of vertebra of *Python*.   *c*, centrum; *poz*, postzy-gapophysis; *prz*, prezygapophysis; *za*, zygantrum; *zs*, zygosphene.

in any one individual.   Cervical, dorsal, sacral and caudal regions are well marked, except in limbless forms (snakes, apodal lizards Pythonomorphs), there being usually two sacrals in most living spe-cies (occasionally three in some lizards and Crocodilians, and rising to six in some fossils).   Nearly all presacral vertebræ bear ribs, although they are often lacking on atlas and epistropheus, and in Lacertilia and Crocodilia lumbar vertebræ are differentiated from the other dorsals (thoracics) by the absence of ribs.   Usually the

cervicals are distinguished from the more posterior vertebræ by the fact that the ribs, though present, do not extend to the sternum.

The articulation of the vertebræ by zygapophyses is often strengthened by a wedge-shaped process (**zygosphene**) on one face of a centrum which fits in a corresponding cavity (**zygantrum**) on the adjoining centrum (fig. 49). A peculiarity of many reptiles, especially lizards, is that the tail may break at a slight strain, the line of fracture passing through the middle of a vertebra which is weakened by the persistent cartilage in the centrum ('glass snakes').

The history of a vertebra is well known in *Sphenodon* and *Alligator* and to a less extent in some lizards. *Sphenodon* has the same formation of cranial and caudal parts as in the lower groups, (p. 22), the cranials being the more prominent, except in the tail where the two are subequal, the elements remaining distinct for a time. Chondrification begins in the caudineurals and caudihæmals and extends up and down and also laterally in the myosepta, this last part developing the transverse process and the rib. The successive neural arches fuse above the spinal cord, and later separate, with the resulting formation of zygapophyses from the intermediate tissue. Skeletogenous tissue (not cartilage) grows inwards between the centra, forming intervertebral discs, which, except in species with permanently amphicœle vertebræ, restricts and may even cut the notochord. On the ventral side the caudal hæmals are shifted forwards to an intervertebral position and may persist for a time at least in the trunk as intercentra, while in the tail they form curved bars—hæmapophyses and hæmal arches, the latter being the chevron bones. Separate centres of ossification occur in the centra and in the elements of the arches, and for a time neural and hæmal arches are connected with the centra by suture, a condition long persisting in Ichthyosaurs, many Crocodilia and some Chelonia.

FIG. 50.—Five anterior vertebræ of *Sphenodon*, stage "S" (Howes and Swinnerton, '01). *a*, neural arch of atlas; *ac*, atlantean centrum; *cr*, cervical ribs; *d*, dens epistrophei; *e*, centrum of epistropheus; *h*, hypochordal bar of atlas; *np*, neurapophysis; *ns*, neurocentral suture; *nsp*, neural spine.

SQUAMATA.—The number of vertebræ in Squamata varies greatly, the largest number being found in apodal lizards (140) and in some snakes (400). In the older fossils and in geckos and Uropeltids the centra are usually amphicœlous; in other recent species they are procœlous. Intercentra occur in the necks of some Pythonomorphs, but are not known elsewhere. Zygosphenes and zygantra are developed in Ophidia, *Iguana* and some Pythonomorphs on the faces of the neural arches. Snakes have strong ventral processes (**hypapophyses**—fused hæmapophyses) on the anterior centra, and in *Dasypeltis* these protrude into the œsophagus and serve to saw the eggs on which these snakes feed.

There are rarely more than nine cervical vertebræ (a few cretaceous lizards have more); and in serpents, where the first two vertebræ lack ribs, there is no other distinction between cervicals and dorsals. In Ophidia the ribs begin on the third vertebra and continue to the tail. Atlas and epistropheus articulate by a dens epistrophei fused with the epistropheal centrum in Ophidia, but separated from it by a suture in Lacertilia. In many Squamates there is no distinction of thoracic and lumbar regions. The ribs of snakes and geckos are articulated to a single transverse process which, in geckos, has a double condyle for the rib. The ventral ends of the ribs are free in snakes and, in conjunction with the ventral scutes, are important in locomotion. Several of the anterior ribs of lizards are connected with the sternum (fig. 61) and in geckos and Chameleons the posterior ribs of the two sides fuse in the middle line. The dorsal part of each rib is ossified in lizards, the ventral remaining cartilage, a differentiation of vertebral and sternal ribs. *Draco* has the last five or six ribs long and straight, supporting a fold of skin which serves as a parachute. *Lacerta* has thoracic and lumbar vertebræ differentiated.

In correlation with the reduction of the hind limbs in Ophidia, Pythonomorphs and apodal lizards, no sacrum is differentiated in these groups. Other lizards have two separate sacrals. The caudal vertebræ bear chevron bones, usually articulated to the centra.

CHELONIA.—In turtles the vertebral column is relatively short and no lumbar region occurs. The very flexible neck contains eight vertebræ, one or two of which have biconvex centra; the others are pro-, opistho- and amphicœlous. The atlas consists of neurapophysis and subchordal bar, its centrum being joined by that suture of the epistropheus to form the dens. In other vertebræ neural arch and centrum are joined suturally, at least in the young. There are distinct cervical ribs in the embryo, which fuse almost completely with the vertebræ and in some genera are so reduced that they are said to be absent. Of the ten thoracic vertebræ the first is free, the others immovably united to each other, and, except in the Atheca, to the neuralia of the carapace. (Götte claims that the neuralia are not dermal but are developed from the periosteum of the neural spines.)

The first dorsal vertebra bears a short rib which joins the under side of the carapace near the second rib. The next eight ribs are greatly expanded and extend laterally to the margin of the carapace. They are articulated to the anterior ends of the centra in the posterior part of the series, farther forwards their heads are intervertebral. The tenth dorsal vertebra has a very short rib, suturally united to both centrum and carapace. There are two amphicœlous sacral vertebræ, each with its short pair of sacral ribs, connected by suture with both centra and carapace, the sacrum being increased by the inclusion of pre- and postsacral vertebræ (synsacrum). The sixteen to thirty caudal vertebræ are usually procœlous, sometimes opisthocœlous. Their transverse processes join the vertebræ between neural arch and centrum and chevrons are greatly reduced or absent.

CROCODILIA have all five vertebral regions well marked. The oldest members of the order had amphicœle vertebræ, later came those with amphyplatyan

centra, while the more recent species, except those noted below, have procœlous centra. The neural arches are connected by suture with the centra; and cervicals and anterior thoracics have a strong process (**hypapophysis**) on the ventral side of each centrum. All of the cervicals (usually nine), the atlas included (fig. 27) bear bicipital ribs. Between atlas and cranium is an incomplete osseous arch, the proatlas (p. 27), preformed in cartilage, lying dorsal to the spinal cord. The atlas consists of distinct neurapophyses and hypochordal bar, its centrum) as in other Amniotes, forming the dens of the epistropheus. With this condition, the epistropheus cannot be procœlous.

There are about ten thoracic vertebræ, the anterior two or three having distinct di- and parapophyses, bearing bicipital ribs enclosing a well-marked vertebarterial canal. Farther back the two transverse processes unite, although the ribs show capitular and tubercular heads. The anterior ribs are divided into vertebral, intermediate and sternal parts, the middle being incompletely ossified. The two anterior ribs join the sternum proper, while from five to seven of the others join its prolongation, the xiphisternum. The lumbar vertebræ (about five) have well-marked transverse processes, diapophysial in position. There are two amphiplatyan sacral vertebræ, each with its sacral rib, connected by suture with ilium and sacral. The caudal vertebræ, the first biconvex, number thirty or more. The anterior have strong transverse processes, and below are chevron bones, apparently intervertebral in position, but in reality articulating with the posterior ends of their centra.

RHYNCHOCEPHALIA have delicate, usually amphicœle vertebræ, but in a few fossils they are amphiplatyan. In front of the sixth, intercentra usually occur between the centra, but are sometimes lacking in the dorsal region. *Sphenodon* is the only living reptile with persistent intervertebral structures, these tending to reduce the amphicœly of the centra. Thoracic and lumbar vertebræ are distinct. There are from two (*Sphenodon*) to four sacrals. Some of the fossils had enormously long spinous processes on the trunk vertebræ, which in some general bore several cross bars of problematic function (fig. 51). Both cervical and thoracic ribs, the latter with a single head, are movably articulated in *Sphenodon*, in which

FIG. 51.—Vertebra and spinous process of *Naosaurus* (Cope).

genus the ribs bear uncinate processes. The related Thalattosaurs have ribs with a single broad head.

Extinct Reptilian Orders.—The THEROMORPHA have amphicœlous vertebræ, and the intercentra are rudimentary and confined to the cervical and anterior dorsal regions. The cervicals often bear short bicipital ribs; those of the dorsal region being longer and sometimes bicipital, sometimes with a single head. They are sometimes articulated between two vertebræ and sometimes to the neural arches. The sacral vertebræ are from two to four in number.

The vertebræ of the SAUROPTERYGIA are usually amphiplatyan, but sometimes amphicœlous. The regions of the column vary in different genera, the cervicals ranging from 16 to 72, the dorsals from 20 to 30; there are from two
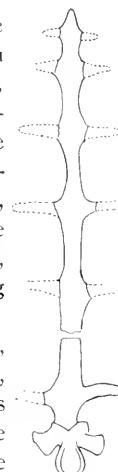
to four sacrals, while there may be forty or more caudals. The neural arches often are not fused with the centra and the hæmal arches of the tail are not complete, the hæmapophyses not meeting below. The short cervical ribs are articulated to the centrum only, while the trunk ribs are single or double headed, the former more common in the older groups.

ICHTHYOSAURIA have numerous (120–150) very short vertebræ, divided into caudal and precaudal regions, there being no sacral region. The precaudals, atlas and epistropheus excepted, bear bicipital ribs which articulate with di- and parapophyses, both on the centrum. The caudal ribs have single heads. Atlas and epistropheus are almost always fused, and in front of and between them are wedge-shaped intercentra. The neurapophyses of the atlas do not meet above and the hæmapophyses in the tail also fail to meet below. A peculiarity of the tail is a strong deflection of the vertebral column, the axis entering the lower lobe of the caudal fin, thus reversing the conditions of the heterocercal tail of fishes.

Some DINOSAURIA have amphicœle, some opisthocœle and some amphi-platyan vertebræ, and different kinds of centra may occur in the same column. All five regions are differentiated, both cervical and caudal sometimes being very long. Atlas, epistropheus and one or two anterior cervicals are fused in some Sauropods and there is no suture between cervical ribs and vertebræ. The thoracic ribs are very long, sometimes with vertebral, intermediate and sternal portions. The sacrum includes from two to six fused vertebræ and some stegosaurs had a synsacrum, vertebræ being added from lumbars and caudals, sometimes to the number of ten. This synsacrum is correlated with the great size of the body, the small fore limbs and the bipedal locomotion. Also, in correlation, is the great size of the vertebral canal in the sacrum, indicating that the spinal cord here was larger than the brain. Another correlation is the fusion of the spines of the sacral vertebræ and the connexion of the neural arches with the iliac bones, dorsal to the sacral ribs. These sacral ribs were often separate, and in *Ceratosaurus* they alternated with their centra. Many Dinosaurs have several caudal ribs and in *Diplodocus* the chevrons are double, each with anterior and posterior branches. In some the longitudinal ligaments (p. 19) were ossified.

PTEROSAURIA have procœlous presacrals, the caudals being amphicœlous. There were seven cervicals, twelve to sixteen dorsals and from four to seven synsacrals. The cervical ribs (sometimes absent), are bicipital; other ribs have one head and are sometimes coossified with the centra as are the neural arches. Sacrals and synsacrals are usually fused; chevron bones occasionally occur in the tail.

AVES.—In birds cervical, thoracic, sacral and caudal regions are always present, but the lumbars are absorbed in the synsacrum to a greater or less extent. *Archæopteryx* and *Ichthyornis* have slightly amphicœle centra as do the embryos of existing birds, the caudals of other birds, and the thoracic vertebræ of penguins, plovers, auks,

some cormorants and gulls. Only the atlas is ever procœlous. All other centra have saddle-shaped (**heterocœle**) ends, the anterior end being concave from right to left, convex dorso-ventrally, the posterior end having these outlines reversed, the saddle shape being most marked in the neck (fig. 52). As a result sagittal sections of a centrum appear as if opisthocœlous; horizontal sections as if procœlous.

The neural arches bear zygapophyses, the postzygapophysis overriding the prezygapophysis of the next vertebra. Each anterior vertebra has dia- and parapophyses. The cervical vertebræ (from eight or nine up to twenty-five in swans, fourteen or fifteen being usual) have elongate centra and usually all are free and very mobile, the exceptions being the fused atlas and epistropheus of hornbills or the union of the last cervical with the first thoracic (tinamous, etc.). Atlas, epistropheus and dens are as in all Amniotes, and
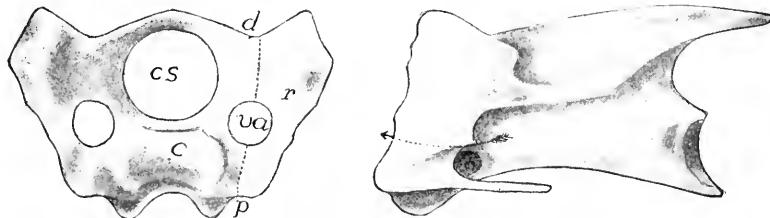
Fig. 52.—Front and side of cervical vertebra of fowl showing cervical rib. *c*, centrum; *cs*, spinal canal; *d*, diapophysis; *p*, parapophysis; *r*, rib; *va*, vertebrarterial canal, arrow passing through it in side view.

these, like all cervicals, bear short ribs with well-developed vertebrarterial canal, the ribs long remaining distinct in Ratites and permanently so in Archæopteryx. The rib of the last cervical, which does not reach the sternum, usually has an uncinate process.

The thoracic vertebræ, six to ten in number (twelve in *Archæopteryx*) are usually more or less fused (not in *Archæopteryx*), strengthening the thorax. The last thoracic (sometimes several of them) may be free, these having saddle-shaped ends, and in diving birds may have bifurcate hypapophyses. All of the thoracic vertebræ have bicipital ribs (single headed in *Archæopteryx*) articulated to di- and parapophyses. These ribs are fully ossified and are divided by a joint into vertebral and sternal parts. At least the anterior ribs (except in some Lamellirostres and *Archæopteryx*) have uncinate processes on the vertebral part, arising as discrete cartilages, which, except in moas and many water birds, fuse later with the ribs, giving

additional strength to the thoracic basket.   No living birds have free lumbar vertebræ, these being included in the synsacrum (fig. 53). The two true sacrals (three in *Struthio* and *Apteryx*), lying just behind the fossæ for the kidneys, are united to the greatly elongate ilium by sacral ribs.   The number of synsacrals is three in *Archæopteryx*, the lowest in living birds is nine and there may be twenty (cassowary).   The bipedal life, the obliquity of the body axis and the necessity of a firm attachment of vertebral column and pelvis are the causes of the synsacrum.

In all modern birds the tail is very short, but is long and lizardlike in *Archæopteryx*, with about twenty elongate centra, movably articulated with each other.   *Hesperornis* has twelve centra, the last few being fused to an imperfect pygostyle.   In modern birds there are usually five or six free caudals followed by four to six (free in the embryo) fused to a single mass, the **pygostyle** (urostyle, ploughshare bone).

MAMMALIA.—There has been no recent work on the ontogeny of the mammalian vertebræ; it is known that the arches belong to the caudal half sclerotomes, but not to what extent the cranial halves contribute.   It is probable that the latter form a considerable part in the tail, although the neural arch springs from most of the length of the centrum.   In development chondrification extends to the intervertebral tissue, the column for a time being a cartilage continuum, only separated into vertebræ at the time of ossification which begins on the inside of the cartilage (endochondrostosis) without the external osseous plates which are so common in many lower Vertebrates.   The arches ossify first, and there are separate centres for epiphyses, transverse processes, zygapophyses and neural spine, the phylogenetic significance of which is unknown.

In all mammals (except Cetacea and Sirenia which lack a sacrum) all five vertebral regions occur.   The usual number of vertebræ is

Fig. 53.—Synsacrum and pelvis of hawk. *il*, ilium; *is*, ischium; *p*, pubis; *pp*, pectineal process; *s*, sacral ribs.

about thirty-five, there being twenty-six in some bats, forty in *Cho-læpus* and *Hyrax* and over eighty in some genera. As a rule the centra are amphiplatyan, but the cervicals and some trunk vertebræ of many Ungulates are opisthocœlous. Each centrum has an epiphysis at either end (poorly developed in Monotremes and Sirenia), and (except atlas and epistropheus), the centra do not articulate directly, but a fibrocartilage disc (**meniscus, intervertebral ligament**) intervenes, this containing the only remains of the notochord as its **nucleus pulposus.** Intercentra are rare, occurring in the lumbar region of some Insectivores.

The neural arches, which arise from the whole length of the centrum, are fused with the centra in the adult, the suture persisting for some time in Monotremes. The spinal nerves make their exit between the neural arches which are notched for their passage, the notches of two adjacent vertebræ forming the **intervertebral foramina.**

Neural arches are present upon all except the posterior caudals, while hæmal arches (chev bones) occur on the anterior caudals, and their homologues occur as hæmapophyses on some presacral vertebræ in a few forms. The chevrons sometimes are fused with their centra, sometimes articulate with reduced hæmapophyses and occasionally are incomplete arches, the hæmal spine being absent.

Excepting the caudal vertebræ and passing by for the moment, the cervicals, the vertebræ bear diapophyses (transverse processes), but the parapophysis is represented by a shallow facet on the centrum for the capitular head of the rib. In some cases the facet is divided (**demi-facets**) between the centra of two adjacent vertebræ. In the presacrals the neural arch bears both pre- and postzygapophyses, and in a few groups the articulation of the vertebræ is strengthened by other processes, most common being a **metapophysis** above the prezygapophysis, an **anapophysis** below the postzygapophysis. These are most frequent in Carnivora and Edentates (fig. 54); American members of the latter group often have other articulating
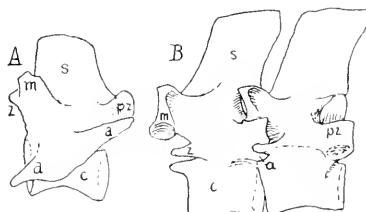
FIG. 54.—*A*, second lumbar vertebra of dog; *B*, second and third lumbars of *Myrmecophaga* (Zittel, '92). *a*, anapophysis; *c*, centrum; *d*, diapophysis; *m*, metapophysis; *pz*, postzygapophysis; *s*, spinous process; *z*, prezygapophysis.

4

surfaces.   Increase in length of the centra with growth of the animal
is provided for by separate centres (**epiphyses**) on either end of the
centra, these being but little developed in Monotremes and Sirenia.
Other epiphyses are common at the tips of the larger vertebral
processes.

The cervical vertebræ of mammals are remarkably constant in
number, the only exceptions to the rule of seven are six in *Manatus
australis* and *Cholœpus hofmanni*, eight in *Bradypus torquatus* and
nine in *B. tridactylus*.   The great variations in the length of the
neck (longest in giraffes, shortest in whales) is solely the result
of the length of the centra.   The longer the neck, the more mobility,
and with this there is a reduction of the zygapophyses.   The cervi-
cals of Cetacea are reduced to thin discs, which, like those of some
Edentates, are frequently fused.

The atlas consists of only the neural arch, the 'hypophysial
bar,' and an expanded 'transverse process' (cervical rib) perforated
by the vertebrarterial canal.   It has no neural spine.   Its centrum
forms the dens of the following vertebra (epistropheus) around which
the atlas turns.   Many mammals have a foramen in the neural
arch for the spinal nerve.   The epistropheus has a large neural
spine which affords attachment for ligaments connecting the verte-
bral column and the cranium.   The dens epistrophei (odontoid
process) may be cylindrical, conical or spoon-shaped.

The number of trunk vertebræ ranges between 16 in some bats,
19 in Artiodactyls, 20-21 in Carnivores, 23 in Perissodactyls and up
to 30 in Hyracoids.   These are divided into thoracic and lumbar
vertebræ, increase in one category in a given region being at the
expense of the other.   The thoracic vertebræ (varying between 9 in
Hyperoodon and *Tatusia*, 21 in *Hyrax* and 24 in *Cholœpus*), are usually
13 in number and are characterized by bearing ribs.   All have strong
neural spines, leaning forwards in front, backwards in the hinder
part of the region.   The lumbars (varying from 2 to 9) have strong
diapophyses, are stout, and, in some groups, may have the additional
articulating processes referred to above (p. 49).

The sacrum (absent from Cetacea and Sirenia) includes from two
to eight or ten vertebræ (*Glyptodon, Dasypoda*) of which but two are
true sacrals, the others being synsacrals added from the caudal
region.   In the sacrum centra and neural arches are often fused,
and frequently the neural spines as well.   The true sacrals bear

ribs, distinct in the young, but fusing early with the diapophyses. The synsacrals often are but slightly modified from the caudal type. The pelvis is articulated by the ilium to the anterior part of the sacrum, while the ischium may be connected with it by ligaments or (Edentates) even be ankylosed.

The caudal vertebræ are very variable in number. The more anterior usually retain neural arch and spine, and hæmal arches on the ventral side. Towards the tip of the tail the vertebræ undergo gradual reduction so that near the end only the centra remain.

Ribs occur in the cervical and thoracic regions, less distinct in the sacrum. They are moveable only in the thoracic region, while in the neck, as in most other Tetrapoda, they are fused with the centra in the adult, although separate in the young. The cervical ribs are the transverse processes of human anatomy. In the young they have both capitular and tubercular heads articulated to distinct dia- and parapophyses, the only place in mammals where the latter exist as *outgrowths* from the centra. The sacral ribs are two in number and are fused with their centra in the adult. The thoracic ribs are flat or slightly rounded, have both heads, the upper reduced to a tubercle. They are divided into two groups, true ribs which reach the sternum, with which they are articulated between the sternebræ; and false ribs ending freely between the intercostal muscles. The true ribs, as a rule, have only the proximal part ossified (**vertebral rib**) that part which joins the sternum (**sternal rib**) persisting as cartilage, but in Monotremes, dolphins and Xenarthra the sternal rib is bone. Occasionally an intermediate section occurs.

Usually the true ribs exceed the false in number, but whales have, at most, but seven true ribs, while in the whalebone whales the sternum is reduced to the presternum which is reached by only the first pair of ribs. Mammals lack an uncinate process on the ribs.

STERNUM

The sternum or 'breastbone' is a skeletal structure, preformed in cartilage, lying in the mid-ventral wall of the cœlom. In many Ichthyopsida it is connected with the pectoral girdle, and in most Amniotes with both girdle and ribs. It has been regarded as peculiar to Tetrapoda and it has been questioned whether the sternum of Amphibia be homologous with that of Amniotes, because the usual

statement is that the Amniote sternum arises from the fusion of cartilages derived from the ventral ends of the ribs. In Amphibia the ribs never approach the sternum.

To understand the questions involved a slight review of the development in mammals where it is best known, is necessary. In this group there is a condensation of mesenchyme in the mid-ventral line, between the two halves of the secondary pectoral girdle which have replaced the coracoidal structures of the lower groups (p. 250). This condensation becomes procartilage and eventually chondrifies. At about the same time a pair of procartilage bars extend back on either side, at first entirely independent of the ribs (fig. 55, *A*). Later these unite with the ribs (*B*) and with the anterior procartilage, and still later with each other, the union progressing backwards. The posterior part of each bar remains unconnected with the ribs. The median anterior procartilage is the
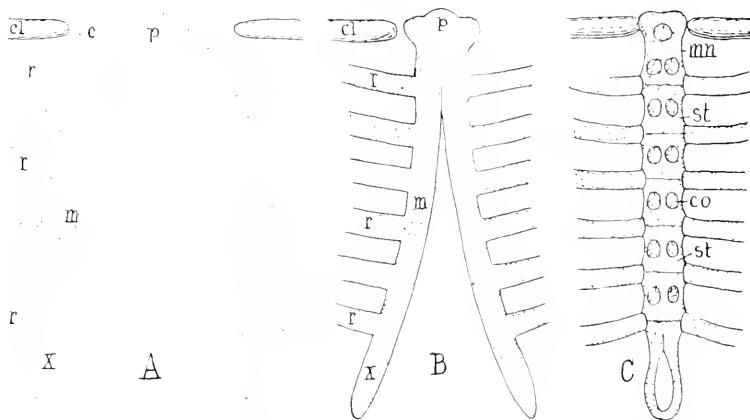
FIG. 55.—Scheme of development of mammalian sternum. *A*, early stage; *B*, cartilage, the halves beginning to unite; *C*, beginning ossification. *c*, ?coracoid procartilage; *cl*, clavicle; *co*, centres of ossification; *m*, mesosternal parts; *mn*, manubrium; *p*, presternum; *r*, ribs; *st*, sternebræ; *x*, xiphisternum.

presternum (it may contain some coracoid elements); the part with the ribs is the mesosternum, while the posterior rib-free portion is the xiphisternum (metasternum, ensiform process). Centres of ossification in the continuous cartilage are irregular in number and arrangement, but what evidence there is points to a typical arrangement of a single centre in the presternum and a series of pairs of centres in the mesosternum, the pairs alternating with the attachment of the ribs (fig. 55, *C*). In the adult of many mammals the most anterior mesosternal centres fuse with the presternal, giving rise to a single bone, the manubrium. The other centres unite in pairs to a series of bones, the sternebræ, which alternate with the ribs. In the xiphisternum the ossification is more or less incomplete. In many mammals the sternebræ remain separate through life, in others they may fuse to a single mesosternal bone, the corpus sterni (gladiolus).

ICHTHYOPSIDA.—Several sharks (fig. 56, *A* and *B*) have a medial cartilage between the coracoidal parts of the pectoral girdle which, apparently is homologous with the mammalian presternum, but its development is unknown. A similar structure is known as high as the reptiles and Dipnoi, but none is known in Teleosts, while in many Urodeles a sternal cartilage occupies the same position (fig. 57) its anterior margins being grooved to receive the postero-lateral
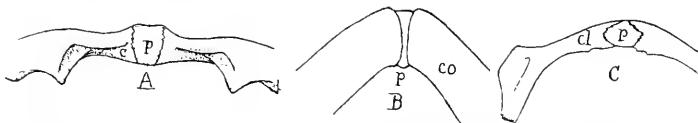
FIG. 56.—Parts of the pectoral girdle of (*A*), *Acanthias; B. Hexanthus* (White) and C, *Nothosaurus* (Zittel, '92). *c, co,* coracoid; *cl,* clavicle; *p,* presternum.

borders of the coracoids. Some Urodeles lack all sternal structures, and none are found in Gymnophiona or in the Stegocephals, the episternum of the latter group being a membrane bone of the pectoral girdle.
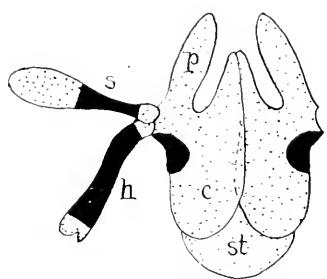
FIG. 57.—Sternum and pectoral girdle of *Siren* (Cope, '89). *c,* coracoid; *h,* humerus; *p,* precoracoid; *s,* scapula (bent outwards); *st,* sternum; cartilage stippled, bone black.
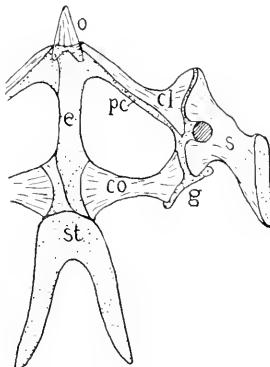
FIG. 58.—Pectoral girdle and sternum of "*Calamites*" (Parker, '68). *cl,* clavicle; *co,* coracoid; *e,* epicoracoid; *g,* glenoid fossa; *o,* omosternum; *pc,* precoracoid; *s,* scapula; *st,* sternum.

The lower Anura (Arcifera) resemble the Urodeles, there being a presternum which embraces the median parts of the coracoids and sometimes (some Hylids, fig. 58) is prolonged backwards as a pair of horns which recall the mesosternal bars of the developing mammal. In the higher Anura (Firmisterna), the epicoracoids of the two sides meet in the middle line and sternal structures occur in front of and behind the girdle, (fig. 58). The anterior of these is commonly

called an **omosternum** (Gaupp calls it episternum, although it is cartilage in origin). Behind the coracoids is a median structure, apparently presternal, which has been called xiphisternum. Both pre- and omosterna are partly cartilage, partly ossified. Nothing is known of their development, and it is uncertain whether they are ever connected.

REPTILIA.—Several fossil groups of reptiles (Phytosaurs, Pseudosuchia, Ichthyosaurs, Sauropterygia,[1] and most Dinosaurs and Theromorphs) have left no traces of sterna, and if one were present it must have been cartilage. Chelonia, with their external armor, and Ophidia which use their ribs in locomotion, and some limbless lizards have none. A few Theromorphs (*e.g. Keirognathus*, fig. 59) had a broad presternum and several Dinosaurs have a pair of oval or hatchetshaped ossicles regarded as sternal. Pterosaurs have a broad thin sternal plate between the ventral ends of the coracoids (fig. 60)
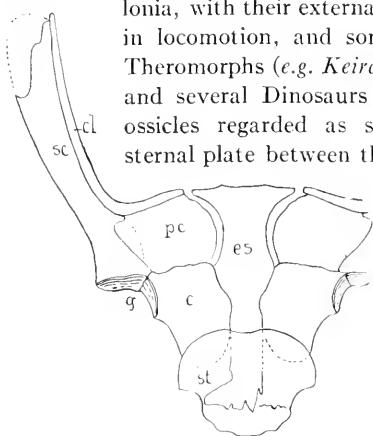
FIG. 59.—Pectoral girdle and sternum of *Keirognathus* (Seeley, '88). *c*, coracoid; *cl*, clavicle; *es*, episternum; *g*, glenoid fossa; *pc*, precoracoid; *sc*, scapula; *st*, sternum.
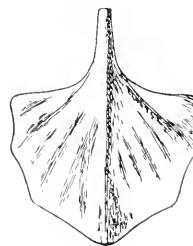
FIG. 60.—Sternum of Pterodactylus (H. von Meyer, '60).

which is prolonged in front as a spine, this thicker and continued back on the broader part as a keel on the ventral surface. In other groups where a sternum exists it never has a part in front of the clavicles comparable to the Anuran omosternum.

The sternum of normal lizards is usually calcified cartilage and is a broad rhomboid plate to which from two to four ribs are attached. It is sometimes entire, sometimes perforated by one or two fenestræ (fig. 61). Behind it is prolonged by a pair of xiphisternal horns, apparently comparable to those of other groups, although they may be connected with one or more pairs of ribs. The anterior border is grooved to receive the coracoids. The sternum of *Sphenodon* (fig. 264) differs little from that of normal lizards.

[1] *Nothosaurus* (fig. 56, C) possibly has a presternum between the clavicles; it is usually called an episternum.

In apodal lizards the sternum is reduced, (even absent) and usually is not connected with the ribs. Sometimes it is continued far back
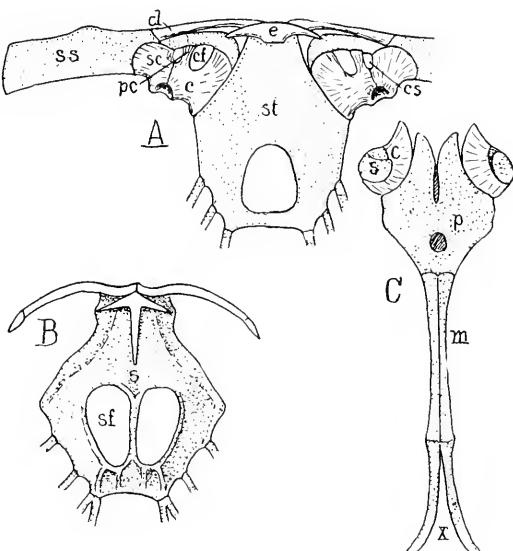
FIG. 61.—Pectoral girdles and sterna of (A) *Phrynosoma* (Fürbringer, '00); (B) *Agama* (Siebenrock, '95) and (C) *Chirotes canaliculatus* (Parker, '68).

as a pair of parallel xiphisternal bars (fig. 61, C). Pythonomorphs have a triangular unossified sternum.

The sternum of recent Crocodilia (calcified cartilage) has the three parts—manubrium, meso- and xiphisternum, the first quadrate in outline with an episternum on its ventral surface (fig. 62). The mesosternal bars may be largely separate, or may unite through-out. In most species the xiphisternal parts diverge, but in *Caiman* they are united distally.

Characteristic of reptiles is another sternal element, the **episternum** or **interclavicle**, a membrane bone which shows no trace of being a paired structure. It lies on the ventral side of the sternum and connects laterally with the clavicles of the two sides. Its shape varies greatly (figs. 61, 62, 265) being a longitudinal or transverse
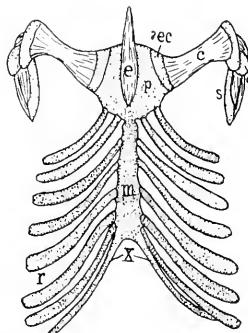
FIG. 62.—Sternum and pectoral girdle of *Crocodilus acutus* just before hatching (W. K. Parker, '68). *c*, coracoid; *e*, episternum; *ec*,? epicoracoid; *g*, glenoid fossa; *m*, mesosternum; *p*, presternum; *s*, scapula; *x*, xiphisternum.

rod, T-shaped, cruciform, rhomboidal, etc., in outline. It is sup-
posed to have arisen from structures like the ventral scales of
Stegocephals and has been homologised with the entoplastron of
turtles.

AVES.—The avian sternum (fig. 63) is usually more or less quad-
rangular or rhomboid in outline and is connected with more ribs
than in reptiles. In the flightless Ratites (fig. 63, *A*) its vaulted
lower surface is smooth and its margins are entire or with a pair of
short horns. In all other living birds (Carinates, *B —E*) a strong keel
(**carino**) is developed on its ventral side, increasing the surface for
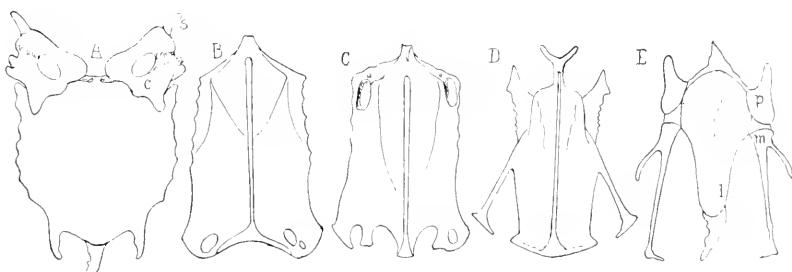
FIG. 63.—Sterna of birds (Selenka, '91, and Shufeldt, '82, '09). *A, Struthio;*
B, Circus; C, Cathartes aura; D, Eremophila alpestris; E, Centrocercus young, showing
developing parts and processes. *c*, coracoid; *l*, lophosteon; *p*, pleurosteon; *m*, met-
osteon; *s*, scapula.

attachment of the muscles of flight. Many have an entire sternum,
but frequently there are fenestræ, or these may extend to the margin,
causing embayments bordered by horns of varying length, features
of little morphological importance.

The sternum arises, so far as known, by a pair of procartilages
between the ribs, these soon fusing in the median line. Ossification
proceeds from two to five centres, and in the adult practically the
whole is ossified. There is nothing to show that the horns separating
the gaps in the postero-lateral border are xiphisternal in character
as is often assumed.

MAMMALIA.— In this class the sternum is usually elongate and
much narrower than in reptiles or birds, and generally the number
of ribs which reach it is greater than in those classes. The develop-
ment has been outlined above (p. 52). It has a weak carina in
bats and some fossorial forms and only in Monotremes (fig. 274) and
tapirs does the presternum persist as a distinct structure, although
when the manubrium extends in front of the first pair of ribs this

anterior part is probably presternal. Manubrium, mesosternum and xiphisternum are usually differentiated, the exceptions being noted below. The xiphisternum is never reached by the ribs; it takes various shapes and is ossified to varying extents. As a rule the sternebræ remain separate (fig. 64) with fibrous or even synovial joints between them, or they may fuse, the extreme being a single mesosternum as in most Primates. The xiphisternum (lacking in *Ornithorhynchus*, Cetacea and sloths) is rarely forked (some Edentates) but may have fenestræ.

Among Edentates the sternum presents several peculiarities. In Manids, which have a greatly elongated tongue, the xiphisternum is extremely long, terminating, in the Asiatic species in a broad, spade-shaped plate; in the African species it forms two long and slender bars which reach to the pelvic region where the two are united. In both groups, and in the Myrmecophagidæ where the sternum is long, some tongue muscles are attached to these extensions. *Tamandua* has strong ventral processes developed from the sternebræ, and the ribs articulate with these as well as intersternebrally with the sternebræ.

FIG. 64.—Pectoral girdle and sternum of mouse, near birth (W. K. Parker, '68). *a*, acromion; *cl*, clavicle; *g*, glenoid fossa; *p*, presternum; *pc*, preclavia; *s*, spine of *sc*, scapula; *ss*, suprascapula; *st*, sternebræ; *x*, xiphisternum.

In Rodents the sternum is often prolonged as a pair of horns in front of the preclavia which are spoken of as episternal, although preformed in cartilage. In whales, where the fore limbs have largely lost locomotor functions, the sternum is greatly reduced. In Odontocœtes there are three separate sternal bones, usually called sternebræ, although usually reached by seven pairs of ribs. Mystacocetes have but a single bone, the manubrium, to which but a single pair of ribs are attached, and which is sometimes continued back by a 'xiphisternal' process. The Sirenian sternum consists of ossified manubrium and xiphisternum, while the mesosternum, connected with three pairs of ribs, persists as cartilage.

SKULL

The skull is a distinctly vertebrate structure, nothing like it occurring in any Invertebrate, while *Amphioxus* alone of the lower Chordates has anything even remotely resembling it. *Amphioxus* has a number of skeletal bars supporting the cirri around the mouth, their bases forming a ring around the oral opening; and there are

slender bars between each two primary gill-clefts, but it is difficult to compare these with any parts of the vertebrate skull.

In lower Vertebrates the skull is readily separable into two very distinct parts,[1] a **cranium** consisting of the case containing the brain, and the capsules around the organs of special sense—nose, eyes and ears. The other part, the **visceral skeleton,** consists of a series of bars (**visceral arches**), an arch between each two visceral clefts (including the mouth) and an arch behind the last cleft. In the higher vertebrates the distinction between these two parts of the skull is hardly evident at the first glance.

Both cranium and visceral skeleton are outlined in cartilage, and in Cyclostomes and Elasmobranchs never pass this stage. In all higher classes more or less of the cartilage is transformed into bone, and these cartilage bones are supplemented by other bones of membranous origin, this holding especially for the cranial roof and the jaws. As a rule, the higher in the scale, the greater the extent of ossification, but the number of separate bones is greater in most lower groups than in the higher, the result, in part, of fusion, in part of complete loss of bones which occur in the lower forms.

Formerly the skull was regarded as a complex of fused and differentiated vertebræ (Vertebral theory of Oken and Owen), the vertebræ being modified by the great size of the brain, by the inclusion of the organs of special sense, and by the development of the anterior part of the alimentary canal. In its broader features this idea was overthrown half a century ago, but that vertebræ are included in the cranium is beyond doubt, for it is distinctly composed of an anterior non-vertebral part, and a posterior part in which several vertebræ are easily seen in the embryo (fig. 65). No sclerotomes are recognized in front of the ear, while behind it their individuality is soon lost, the resulting mesenchyme forming a continuous layer between the brain on one side and the myotomes and epidermis on the other. From this continuum enclosing the whole brain and the sense organs, the cranial structures are developed.

The visceral arches do show a marked metamerism, as do the visceral clefts between which they lie, but whether this metamerism corresponds to that of the trunk or is a special 'branchiomerism' has not been settled, although the former seems more probable. Another question is whether the whole visceral part belongs to the head. On the one hand is *Amphioxus* where the very numerous clefts extend from near the tip of the head through nearly half of the body. In Cyclostomes the clefts may number fourteen, all being supplied by branches of the vagus (tenth cranial) nerve, the last lying some distance behind the brain. The number of clefts and arches diminishes progressively in ascending the

[1] Recently the terms **neurocranium** and **viscerocranium** have been introduced for these. Strictly speaking the cranium is neural, and thus the term is used here.

Vertebrate scale, the lowest sharks having eight (not including the mouth) while in higher Vertebrates the number is five or six.   This variation in number may be explained in two ways.   In the higher groups there has been a loss at the posterior end of the series; or in all Vertebrates there is a zone of vegetative growth at the junction of head and trunk, and the amount of growth at this point has been more and more limited as the phylum has developed.   Certain it is that the two preotic arches (mandibular and hyoid) belong to the head, and as the relations of these are similar in most respects to the arches behind the ear, probably all arches belong to the head.

Chondrocranium

In the following outline of the development and structure of the skull, only those features are included which are common to all Gnathostomes, the Cyclostome skull being considered separately (p. 78). The simplest picture, so far as cartilage parts (**chondrocranium**) are concerned is furnished by Elasmobranchs which are here used as a basis.   But since the head of a shark is strongly flexed in the early embryo before skeletal parts appear (fig. 86), the early skull is described here as if extended in a straight line with the notochord, a condition largely regained in the adult.

In the embryo (fig. 65) the noto-chord extends into the head as far as the infundibulum and its associated ectodermal structure, the hypophysis. On the supposition that vertebræ are only formed around the chorda, only those parts of the skull behind the hypophysis can be vertebral, but whether there be any vertebræ as far forwards as this has not been shown. This limitation of the tip of the notochord allows the cranium to be divided into chordal and prechordal parts.

FIG. 65.—Early chondrocranium of an Elasmobranch, straightened; compare with fig. 86. *als*, spheno-lateral; *ctr*, trabecular cornua; *ep*, ethmoid plate; *fhyo*, hypophysial fenestra; *oc*, otic capsule; *ov*, occipital vertebræ; *n*, notochord; *pc*, parachor-dals; *tr*, trabeculæ.

In the chordal part a plate of (**parachordal**) cartilage arises on either side of the notochord, extending as far laterally as the tissue

below the developing ear (otic vesicle). The two parachordal plates form the floor of the hinder part of the cranium, and, increasing in thickness, the plates meet, at first below, later above the notochord, so that a **basal plate** is formed, the notochord included in the cartilage.

It is a question as to how far the basal plate is segmental. In the early stages the part behind the level of the otic vesicles is often metameric in outline, while the union of the parachordals ventral to the notochord recalls the hypochordals of vertebræ, possible indications that here are coalesced vertebræ, the number of which varies in different Vertebrates. The actual vertebral arches of the postotic region are considered below.

The basal plate extends as far forwards as the tip of the notochord. A little later than its appearance two longitudinal bands of cartilage develop on either side, beneath and lateral to the brain and in front of the basal plate. The lower pair of these, the **trabeculæ cranii,**
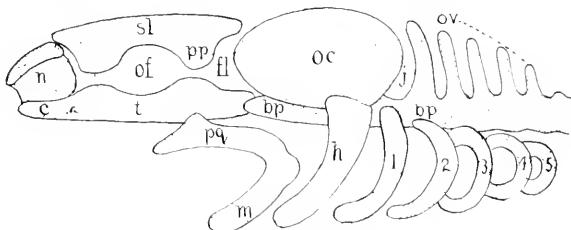
Fig. 66.—Diagram of developing skull of *Acanthias.* *bp*, basal plate; *c*, trabecular cornu; *fl*, foramen lacerum; *h*, hyoid arch; *j*, jugular foramen; *m*, Meckel's cartilage; *n*, roof and wall of nasal capsule; *oc*, otic capsule; *of*, optic fissure; *ov*, occipital vertebræ; *pp*, preotic pillar; *pq*, pterygoquadrate; *sl*, sphenolateral cartilage; *t*, trabecula; 1-5, branchial arches.

are slender bars which lie, one on either side of the hypophysis and ventral to all preotic nerves. As they increase in length they meet in front of the hypophysis, forming by their junction a horizontal cartilage, the **ethmoid plate,** beneath the anterior end of the brain. At about this time the hinder end of each trabecula fuses with the antero-lateral angle of the basal plate; trabeculæ, ethmoid and basal plate forming a ring around the hypophysis, the opening being the **hypophysial fenestra.**

The more dorsal bars in front of the basal plate are the **spheno-laterals**[1] (fig. 66). They parallel the trabeculæ, but lie dorsal to the

[1] These are variously called **alisphenoid cartilages** and **pleurosphenoids** and are represented in part in the higher groups (Amniotes) by the **marginal tænia.**

preotic cranial nerves, of which the second and the fifth afford important landmarks. With increase in age the two bars of a side become connected by cartilage, at first in two places. The more posterior lies just in front of the mandibular nerve and is, in part, the homologue of the alisphenoid bone of the higher groups. In some of the higher Vertebrates the union is very narrow and has been called the **preotic pillar (pila prootica).** When complete, this **alisphenoid cartilage** extends as far forwards as the optic nerve, in front of which is a second (**orbitosphenoid**) cartilage connexion which reaches to the ethmoid region. Thus the optic and some other nerves pass from the brain through an opening, the **primitive orbital fissure,** which is completed above and below by the sphenolateral and trabecular cartilages. The mandibularis branch of the fifth, the sixth and at least a part of the seventh nerves leave the cranium by the gap between otic capsule (*infra*) and the preotic pillar. Later this gap is closed dorsally by a growth of cartilage from the sphenolateral to the capsule, while below the union of trabecula and basal plate completes the wall of the opening (**foramen lacerum**) which transmits the nerves to the exterior. Trabeculæ, sphenolaterals and orbito- and alisphenoid cartilages form the side wall of the brain case in the interorbital region.

In some Vertebrates basal plate, trabeculæ, sphenolaterals and ethmoid plate form as a continuum with small foramina for the exit of the nerves. Usually the mandibularis ramus is eventually included in the alisphenoid cartilage, its opening being the **foramen ovale.** So, too, the optic nerve is often included in the orbitosphenoid (**optic foramen**) while the third, fourth nerves and other branches of the fifth nerve vary in their place of exit, sometimes passing through a **foramen rotundum** in the alisphenoid cartilage.

The parts thus outlined form most of the cartilaginous brain case or chondrocranium, which is completed, not only by the formation of a roof and a more complete floor, arising by growths from the parts enumerated, but by the sense capsules—nasal, sclerotic and otic—which are formed around the three principal organs of special sense.

The trabeculæ continue in front of the ethmoid plate as a pair of diverging horns (**cornua trabecularum**), each cornu lying beneath the corresponding nasal sac and forming the floor of the nasal capsule. The two sacs are usually separated by a median nasal septum, an upgrowth from the ethmoid plate. Each nasal capsule is connected with the interorbital wall by a continuation (**sphenethmoid**

commissure) of the sphenolateral cartilage. The rest of the wall of the nasal capsule arises by outgrowths from septum, cornu, sphenethmoid and a separate cartilage (**antorbital process**) which forms the posterior wall of the capsule and soon joins the rest of the cranium. The cavity of each nasal capsule is connected with the cranial cavity by an **olfactory foramen** through which the olfactory nerve passes from the sensory epithelium to the brain. On the anterior or antero-inferior wall is a large opening, the **naris** (nostril), for the entrance of water to the nasal cavity. Nasal capsules, and ethmoid plate form a trough for the olfactory nerves and the anterior end of the brain.

The eye is surrounded by a similar skeletal capsule, the **sclera,** but as the eye is in continual motion, moved by its muscles, this sclera never unites with the rest of the cranium and so is not usually considered as part of the skull. That it is skeletal is shown by the facts that it is usually of cartilage and in many Sauropsida and a few other forms sclerotic bones are formed in, these being true cartilage bones.

Each **otic** (ear) **vesicle** is similarly enclosed in a cartilage **otic capsule,** which begins, in sharks, as an upgrowth from the lateral part of the basal plate, but in other groups may arise independently, the capsules of the two sides in either case forming the side walls of the chondrocranium in the otic region. By gradual additions the capsule is completed by the formation of ends (**cupulæ**), a lateral wall and a roof, while the medial wall (towards the brain) is last to be enclosed and always has foramina for nerves and for the perilymph and endolymph ducts of the ear. The interior of the capsule becomes complicated to form the **otic labyrinth** which will not be described here.

The posterior part of the cranium is formed by vertebral arches, varying in number in different groups and separated by the trunks of the postotic nerves. These arches gradually extend upwards, the most anterior pair joining the capsule above, completing the **jugular foramen** through which usually the ninth and tenth nerves and the jugular vein pass. These occipital vertebræ, by continuous growth and by contributions from the otic capsule, form a roof (**synotic tectum**) over the hinder part of the brain, and from this tectum, except in Elasmobranchs, ex- and supraoccipital bones will ossify.

In the higher vertebrates this chondrocranium develops as a cartilage brain case but little farther. In Elasmobranchs (fig. 87)

and some other Ichthyopsida it has a more or less complete roof (**tegmen cranii**) formed by the synotic tectum behind, farther rorwards by growth from the side walls of the interorbital and nasal fegions, all meeting in the medial line dorsal to the brain. The floor is completed between the eyes by growths from the trabeculæ across the hypophysial fenestra, completely separating the hypophysis from the roof of the mouth. In most Vertebrates hypophysis
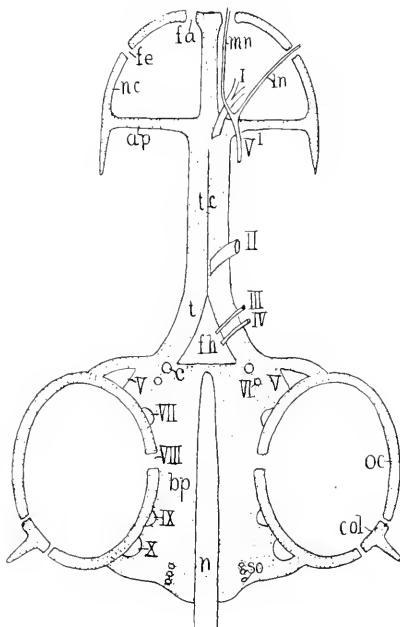
FIG. 67.—Schema of tropibasic cranium (Gaupp, '04). *ap*, antorbital plate; *bp*, basal plate (parachordals); *c*, carotid foramen; *col*, columella; *fa*, *fe*, foramina apicale and epiphaniale; *fh*, fenestra hypophyseos; *ln*, *mn*, lateral and medial nasal nerves; *nc*, nasal capsule; *oc*, otic capsule; *so*, foramina for spino-occipital nerves; *t*, trabecula; *tc*, trabecula communis; II–X, nerve exits.

and infundibulum from this time occupy a pit (**hypophysial fossa**) in the floor of the cranium, fossa and its anterior and posterior borders constituting the **sella turcica** (Turkish saddle), an important landmark in the skull.

The primitive cranium just described undergoes modifications in the higher classes, some of which are described in connexion with the separate groups, but a few general points are summarized here. The primitive chondrocranium is **platybasic** (fig. 131), having a large and wide hypophysial fenestra, and is found only in Ichthyopsida, and there only in species with a depressed head and relatively small

eyes. When the heighth of the head equals or exceeds its breadth, and especially when the eyes are large, the trabeculæ are forced towards the middle line, leaving a small hypophysial fenestra, in front of which the bars of the two sides are fused to a **common trabecula** which continues forwards into the nasal region. This is the **tropibasic cranium,** occurring in many Teleosts, in all Sauropsida (fig. 67) and in a modified form, in Mammalia.

The great size of the eyes and the narrow head also affect the ali- and orbitosphenoid cartilages, especially the latter, which may be so pressed together that they form a thin vertical plate (**interorbital septum),** and only dorsal to the eyes do they retain their individuality as a pair of diverging **supraseptal plates** (fig. 68). This constriction of the cranial cavity also restricts the brain largely or wholly (mammals excepted) to the postorbital part of the cranium, but a part of the anterior cranial cavity can still be recognized in the groove formed by the supraseptal plates, which contains the olfactory nerves (sometimes the olfactory lobes as well) and which is closed dorsally by the frontal and nasal bones. The tropibasic cranium and the greater development of membrane bones in the cranial wall are accompanied by a reduction of the interorbital cartilages (ali- and orbitosphenoids) which become fenestrated (fig. 162) and in some cases they fail to ossify.

FIG. 68.—Schematic section through orbital region of Sauropsidan. *ct.* trabecula communis; *f.* frontal bone; *pt.* pterygoid; *r,* retina; *s,* interorbital septum; *sc,* sclera; *sp.* supraseptal plates; *z,* zygomatic.

In platybasic crania the second to fifth nerves at first leave the skull through the **preotic foramen (f. lacerum)** and through the orbital fissure (fig. 66), but with the extension of the cartilage they may become surrounded by ali- and orbitosphenoids in different ways, it often happening that in the adult neither of the primitive openings allows passage of nerves to the exterior.

CARTILAGINOUS VISCERAL SKELETON

The visceral skeleton arises as a series of cartilage bars in the walls of the anterior part of the digestive tract (mouth and pharynx). At first these are continuous rods of procartilage, right and left, their dorsal ends lying on either side of the cranium and anterior verte-

bræ, but are not connected with any other skeletal structures (fig. 66). Then the ventral ends of each pair unite and the successive arches thus formed become connected in the midventral line by a series of unpaired cartilages (**copulæ**). The series of arches begins just behind the mouth and extends posteriorly to just behind the last gill-cleft, clefts and arches alternating. The arches serve to strengthen the digestive tube which is weakened by the clefts, and also as supports for the gills and for attachment of muscles.

The two anterior arches differ considerably from the rest and have received special names, the first being the **mandibular arch,** the second
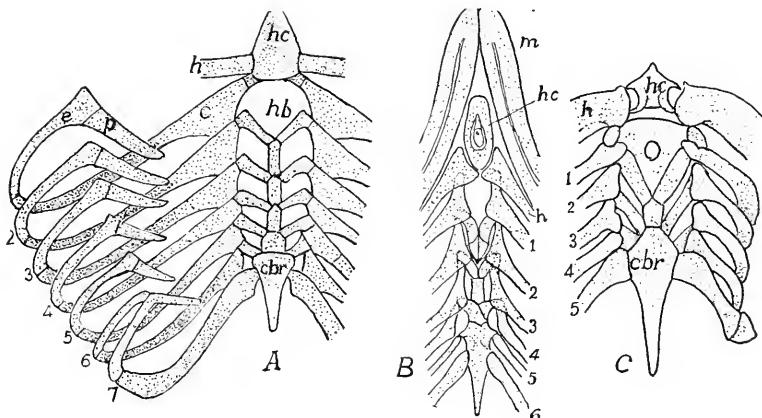
FIG. 69.—Branchial arches of (*A*) *Heptanchus* (Gegenbaur); (*B*) *Chlamydoselachus* (Garman) and (*C*) *Cestracion* (Gegenbaur). *c*, ceratobranchial; *cbr*, cardiobranchial (last copula); *e*, epibranchial; *h*, hyale; *hc*, hyoid copula (basihyal); *m*, Meckel's cartilage; *p*, pharyngobranchial; 1–7, branchial arches.

the **hyoid arch.** The rest are called **branchial** or **gill arches.** The gill arches are at first similar to each other, and as they apparently present the condition from which hyoid and mandibular arches have been derived, they are described first.

Each half of a branchial arch divides early into four cartilages (fig. 69, *A*), named from above downwards, **pharyngobranchial, epibranchial, ceratobranchial** and **hypobranchial** elements, the first lying in the upper lateral part of the pharyngeal wall and the hypobranchial in its floor, the hypobranchials of the two sides being connected by a copula, called a **basibranchial.** Gill arches are usually referred to by number, beginning in front, and are limited by the number of gill-clefts. As a rule the anterior arches are the

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more conservative, the posterior the more variable and the first to disappear.

In all Gnathostomes branchial and hyoid arches arise deep in the pharyngeal walls, medial to the cœlom and its rudiments (fig. 70). In other words they constitute a splanchnic skeleton. As stated above they are usually regarded as belonging to the skull, the position of some behind the limits of the head being explained by shifting, but possibly their innervation by the vagus nerve is the result of several post-cranial nerves becoming associated with the anterior part of the tenth which certainly is a cranial nerve.
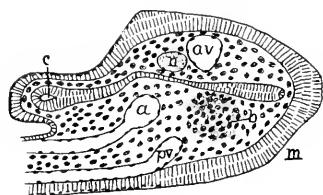
Fig. 70.—Section of gill septum of *Pristiurus* (Dohrn, '84), showing relations of branchial cartilage to remnants of cœlom. *a*, branchial artery; *av*, anterior vein (efferent artery); *b*, procartilage of gill arch; *c*, remains of cœlom, the mesothelial tissue continuing towards medial side of section. *m*, *n*, nerve; *pv*, posterior vein.

The hyoid arch lies between the first true gill cleft and the spiracle (or its homologue in higher Vertebrates, the Eustachian or auditory tube). It divides early into two main parts (fig. 71), a dorsal **hyomandibula,** which in most Elasmobranchs is attached to the otic capsule by ligaments and in many plays a part in the suspension of the jaws. The lower region, the **hyale,** has its two halves connected below by a **basihyal** copula. Sometimes the hyale remains entire, but usually it is divided into three cartilages, the **epi-, cerato-** and **hypohyals.** The hyale largely supports the floor of the mouth, and in higher groups, the tongue as well.

The first (mandibular) arch forms the framework of the mouth in Elasmobranchs (fig. 71), the spiracle lying between it and the hyoid arch. Except in the earliest stages, each half arch is divided into dorsal and ventral parts which meet at a sharp angle at the hinge which lies behind. The dorsal part, the **pterygoquadrate cartilage,**[1] forms the skeleton of the upper jaw of Elasmobranchs and Chondrostei. The lower part—**Meckel's cartilage** or **Meckelian**—is the framework, at least in the early stages, of the lower jaw of all Gnathostomes and the permanent jaw of Elasmobranchs and Chondrostei. The ends of the arch, corresponding to the dorsal and ventral ends of a gill arch—the tips of the upper and lower jaws of a shark— meet

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[1] Often called **palatoquadrate** or **palatopterygoid,** because once thought to be concerned in the formation of the palatine bone of higher Vertebrates. The name adopted here seems preferable, although it is uncertain to what extent it is homologous with the pterygoid process of man.

and may fuse in the median line or may be connected only by ligament. It is said that sometimes a copula exists between the anterior ends of the Meckelian, strengthening its resemblance to the other arches. Pterygoquadrate and Meckel's cartilage articulate behind, forming the hinge of the jaws.
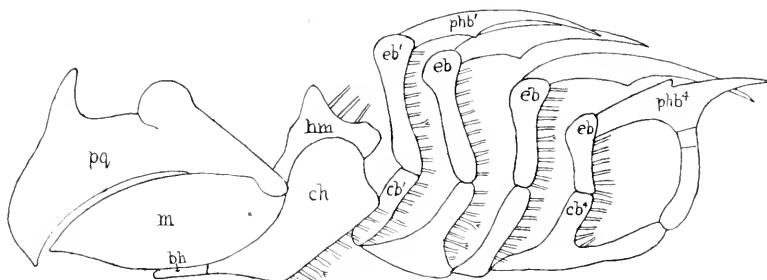
FIG. 71.—Visceral arches of *Acanthias* (Wells, '17). *bh*, basihyal; *cb*, ceratobranchial; *ch*, ceratohyoid; *eb*, epibranchials; *hm*, hyomandibula; *m*, Meckel's cartilage; *phb*, pharyngobranchials; *pq*, pterygoquadrate.

This is a good place to mention the ways in which the jaws are connected with the cranium. Several authors have discussed the different methods of suspension, but possibly the best grouping is that of Gregory ('04). **Holostyly** is characterized by a primitive
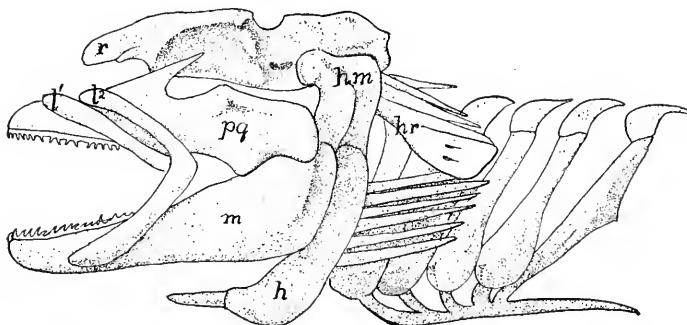
FIG. 72.—Skull of *Squatina* (Gegenbaur). *h*, hyoid; *hm*, hyomandibula; *hr*, hyomandibular rays; *l*, labial cartilages; *m*, Meckel's cartilage; *pq*, pterygoquadrate; *r*, rostrum.

hyoid arch which plays no part in suspension of the jaws, while the pterygoquadrate bar, at first separate from the cranium (fig. 66), fuses with it later so that no line of separation occurs in the adult. This condition is known only in Holocephals (fig. 91). In the

hyostylic group, represented by most Elasmobranchs, Ganoids, and Teleosts, the pterygoquadrate may articulate with the cranium, but never fuses with it. The hyomandibula articulates with the otic capsule at its upper end, its lower end with the quadrate part of the pterygoquadrate, and is thus largely suspensorial (figs. 72, 74, 117, etc.). Several subdivisions of hyostyly are recognized. **Autostyly,** occurring in Dipnoi and Tetrapoda, has at least the pterygoid part of the pterygoquadrate closely connected with the cranium, while the hyomandibula (unless it be the stapes, p. 119) is reduced or lost and is in no ways the suspensor of the jaws.

In most Elasmobranchs, and here and there in higher classes, cartilages occur in front of (external to) the mandibular arch (fig. 72, *l*) the morphology of which is uncertain. In Elasmobranchs these **labial cartilages** lie just outside (morphologically anterior to) the halves of the mandibular arch. The posterior group of these consists of upper and lower halves, hinged like the jaws, while in front of this is only an upper labial on either side.

These labial cartilages have been considered as remnants of visceral arches which, in the ancestral Vertebrate occurred in hypothetical septa between gill clefts anterior to the present mouth. This has little support, aside from their position and the hinge of the posterior labials. Labial cartilages occur as high as the Crossopterygii and possibly the Amphibia.

OSSIFICATION OF THE SKULL

In all Vertebrates above the Elasmobranchs the cartilage skull is reinforced and more or less replaced by cartilage and membrane bones. Since, in all living Vertebrates, cartilage appears before membrane bones, and as the preceding paragraphs give a cartilage framework on which to build, the cartilage bones are described here before the others, although in ontogeny (probably in phylogeny), membrane bones appear before any ossifications in the cartilage.

Names were first given to the bones of the human skull, from which they have been transferred with more or less success to the lower groups, with such changes as necessity has caused. Some single bones in the adult human skull are represented by two or more separate elements in some of the lower classes, while there are numerous instances of piscine, Amphibian or reptilian bones which are absolutely lacking in man. There is a greater difference between the skulls of fishes and Tetrapoda than between the lowest Amphibian and that of man. The bones of the most primitive Amphibians, the Stegocephals, are made the basis of the following account.

Cartilage Bones.—All cartilage bones are laid down as small centres, either on or in the cartilage (peri- or endochondrostoses, p. 7) with no periosteum or perichondrium between bone and cartilage. Sometimes there are two centres in what is here treated as a single bone (basi- and presphenoids, etc.). First to be considered are the bones of the cranium, those of the visceral arches following.

The base (hinder end) of the chondrocranium is perforated by a large opening, the **foramen magnum,** through which the brain connects with the spinal cord. Around this opening four cartilage bones, grouped as **occipitalia,** are developed. These include a
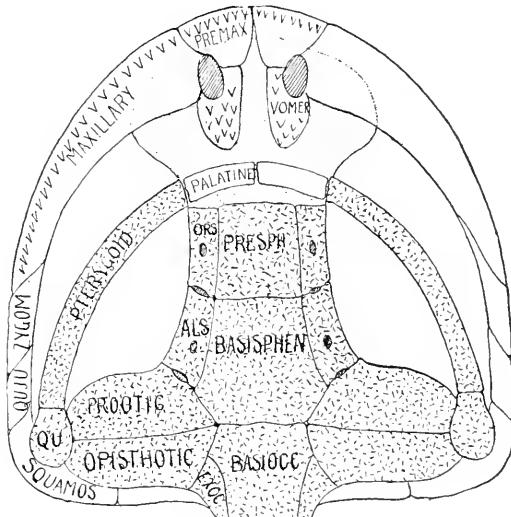
FIG. 73.—Diagram of ventral side of skull; chondrocranium shaded. Cartilage stippled; cartilage bones with lines and dots, membrane bones outlined.

basioccipital below the foramen, ossifying in the hinder part of the basal plate, the notochord passing through it in the early stage. On either side of the foramen is an **exoccipital** (**pleuroccipital**), formed in what would be the neurapophyses of this vertebral part of the cranium. The ring is completed above by a **supraoccipital,** formed in the synotic tectum and the apex of the vertebral arch. The supraoccipital is the only cartilage bone in the cranial roof of any vertebrate.

The **sphenoidalia** (fig. 73) arise in front of the occipitalia. Of these there are two groups, the basisphenoid group just in front of the occipitals, the presphenoid group in front of the other. The

basisphenoid bone extends forwards in the cranial floor from the basioccipital as far as the tip of the notochord. The **presphenoid,** also in the floor, reaches from the basisphenoid to the ethmoid region and hence is largely trabecular in origin. The basisphenoid bears on its anterior dorsal surface the posterior wall (**dorsum sellæ**) of the sella turcica. Anterior to either anterolateral angle of this bone an **alisphenoid** bone ossifies in the lateral wall of the cranial cavity from the posterior ends of trabecula and sphenolateral cartilages and in front of the exit (foramen lacerum) of the fifth and seventh nerves. The presphenoid, in the same way, is associated with an **orbitosphenoid** bone on either side, also developed in the same cartilages, the optic nerve either passing through it (optic foramen) or between it and the alisphenoid in the orbital fissure. The presphenoid forms the floor of the hypophysial fossa and extends forwards to the ethmoid region.

The **ethmoidalia** include a **mesethmoid** ossifying in the ethmoid plate and its dorsal extensions (not mentioned above) while in or near the lateral wall of each nasal capsule is an **ectethmoid,** parts of which, in higher Vertebrates, become coiled to form **conchæ** (**turbinates**) which support the olfactory membrane.

A series of **otic bones** (fig. 73) ossify in each otic capsule which becomes intruded in the angle between basi- and exoccipital behind, and basi- and alisphenoid in front. Most Vertebrates have three of these otica, a **prootic** in the anterior part, an **epiotic** in the roof and an **opisthotic** in the posterior cupula, pro- and opisthotic usually meeting on the inferior side of the capsule. Fishes may have two more otica, a **sphenotic** in front of the others and a postero-lateral **pterotic,** lying over the semicircular canal. Whether there be any traces of these last in higher Vertebrates is uncertain. In the higher classes the otic bones fuse in the adult to a single **petrosal** or **periotic** bone. There is also a tendency for the petrosal to unite with the squamosal (a membrane bone described later) to form the **temporal bone** of mammals. The only other cranial cartilage bones are the **sclerotics** (p. 62) in the outer part of the sclera of the eye.

The cartilage visceral skeleton (especially the first two arches) undergoes considerable modification in the higher Vertebrates. In all classes above the Elasmobranchs and Chondrostei the pterygoquadrate no longer is the skeleton of the upper jaw, this being formed by membrane bones to be described below. With this change in

function there is a tendency for at least the anterior part of this cartilage to be connected, directly or indirectly, with the floor or sides of the cranium or to end freely in front, the connexion between the two sides being lost. Its posterior end, except in mammals, still furnishes the part (quadrate) which enters into the hinge of the jaws.

With ossification a series of bones are formed in this cartilage, the number of which varies in the different classes. In all Vertebrates (mammals excepted) in which the jaws are formed by membrane bones, the hinder end of the cartilage forms a **quadrate bone,** the upper half of the hinge of the jaws. The more anterior part of the
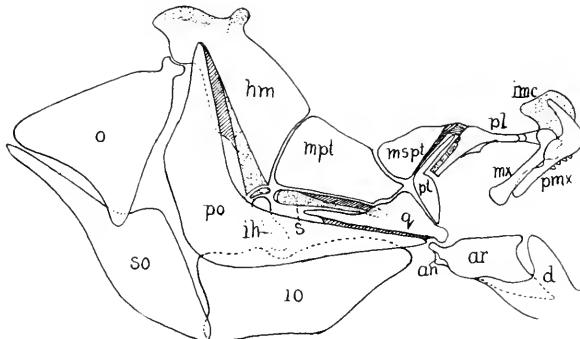
FIG. 74.—Mandibular and hyoid arches and operculum of *Pleuronectes* (Cole and Johnstone, '01). *an,* angulare; *ar,* articulare; *d,* dentale; *hm,* hyomandibula; *ih,* interhyal; *imc,* intermaxillary cartilage; *io,* interoperculum; *mpt,* metapterygoid; *mspt,* mesopterygoid; *o,* operculare; *po,* preoperculum; *pl,* palatine; *pm,* premaxilla; *pt,* pterygoid; *q,* quadrate; *s,* symplectic; *so,* suboperculum.

pterygoquadrate may ossify as several bones. In Teleosts (fig. 74) a part in front of and dorsal to the quadrate forms a **metapterygoid** bone, while in a few bony fishes its extreme anterior end ossifies as an **autopalatine.** A few groups have an **epipterygoid (columella cranii** of lizards, **ascending process** of Amphibia) which extends up from the rest of the pterygoid structures to the alisphenoid cartilage or to the overlying parietal bone (fig. 75).

In the primitive lower jaw (Meckelian) there are at most but two ossifications on either side, and even these do not always develop. At the posterior end, each Meckelian may ossify as an **articulare** which articulates with the quadrate, forming the lower half of the hinge. The other cartilage bone is a **mentomeckelian,** best known in Anura, at the symphysis of the lower jaw. (There is some evi-

dence that the mentomeckelian is derived from the anterior labial of Elasmobranchs, p. 68.)

The cartilage elements of the hyale, in Ichthyopsida, ossify as bones which usually have the same names as the cartilages (p. 66). For the parts in the higher groups reference must be had to the accounts of the separate classes (*infra*). In most fishes the hyomandibular cartilage gives rise to two bones (fig. 74), a **hyomandibula** which usually articulates with the otic region of the cranium, and below this a **symplectic,** which connects with the quadrate; hyomandibula, quadrate and symplectic forming the suspensor of the lower jaw. Above the fishes the fate of the hyomandibula is one of the unsolved problems, one possibility being that it is represented by the stapes, one of the bones of the ear. The branchial arches are greatly modified or degenerate in higher Vertebrates, less so in Ichthyopsida. In so far as they ossify, the resulting bones bear the same names as the cartilages from which they come (p. 65).

Membrane Bones.—The membrane bones of the skull are regarded as derivatives of the skin, arising from scales or teeth, and here the term dermal bones is most applicable, for in some cases, like the sturgeons, there can be little doubt that at least a part of the cranial bones come from the corium of the skin. Farther back in history these bones are believed to have arisen by enlargement or fusion of the bases of placoid scales or their homologues, the teeth (fig. 6). On this supposition it is evident that the number of individual bones would be greater in lower than in higher groups. For our purposes a schematic skull (much like that of a Stegocephal) in which numerous bones occur, affords a good basis for locating the cranial membrane bones (fig. 75).

In all Vertebrates above Elasmobranchs membrane bones form the roof of the brain case, the cartilage roof being greatly reduced or absent. These roofing bones are primitively in pairs, one on either side of the median line. In most Vertebrates the most posterior of these roofing bones is single in the adult and is known as the **interparietal,** which lies just in front of or above the supraoccipital. In some lower forms and in the ontogeny of the higher two bones (**dermoccipitals,** fig. 76) may occupy its place. In higher groups the interparietal is often fused (as in man) with the supraoccipital, sometimes with the parietals. Next in front is the pair of **parietal bones,** with frequently, as in many reptiles and Stegocephals, a

parietal foramen for the parietal organ between them (fig. 76). These are followed by a pair of **frontal bones,** usually lying between the orbits; these in turn being joined in front by the **nasal bones** which roof the nasal region above the ethmoid and bound the nares behind.

With the appearance of bones in the skull, the function of the pterygoquadrate as the upper jaw is taken by dermal bones developed in the upper border of the mouth, these bones at the same time forming the anterior and lateral boundaries of the cranium. At its fullest development this series of bones consists, on either side, of a **premaxilla (intermaxilla, incisivum),** in front, this forming the tip
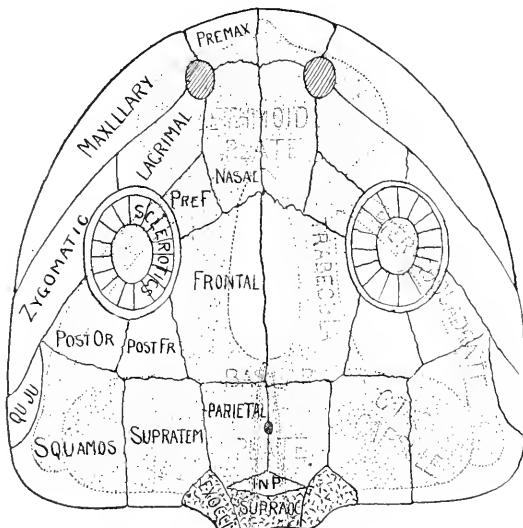
Fig. 75.—Diagram of dorsal side of skull; chondrocranium dotted; cartilage bones with lines and dots; membrane bones outlined.

of the jaw and bounding the naris in front and below. Lateral to the premaxilla is a **maxilla,** maxilla and premaxilla usually being the only tooth-bearing bones in the margin of the jaw, while the maxilla usully forms a part of the lateral (inferior) border of the orbit. The maxilla connects behind with the **zygomatic (malar, jugal)** bone which also forms part of the lateral border of the orbit and is connected posteriorly with a less constant element, the **quadratojugal,** which extends back to .the quadrate and also articulates with the **squamosal bone** which, in the more primitive Vertebrates forms the postero-lateral angle of the cranium. The squamosal overlies the quadrate and is often immovably connected with it.

The squamosal is connected on its medial side with the parietal, sometimes directly, but in the older groups by a **supratemporal bone,** while in the angle between squamosal and supratemporal there is occasionally a membrane bone of uncertain homology, the **tabulare** (fig. 76), often, but erroneously, called the epiotic, the true epiotic being a cartilage bone (p. 70).

The bones so far enumerated surround the orbit, but several bones may intervene between them and the eye. These bones have
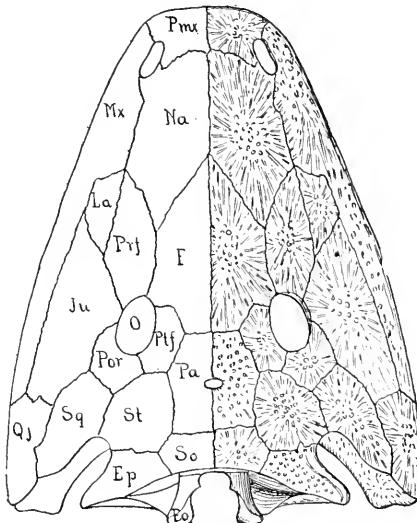
Fig. 76.—Stegocephal cranium (*Capitosaurus*, Zittel). *eo*, exoccipital; *ep*, tabulare (epiotic); *f*, frontal; *ju*, zygomatic; *la*, lacrimal; *mx*, maxilla; *na*, nasal; *o*, orbit; *pa*, parietal; *pmx*, premaxilla; *por*, postorbital; *prf*, prefrontal; *ptf*, postfrontal; *qj*, quadrato-jugal; *so*, dermoccipital; *sq*, squamosal; *st*, supratemporal.

their origin in a series of ossifications which develop around the lateral line canals, an account of which is given in the description of the Teleost skull (p. 94). In the higher groups some of these **lateral-line bones** have received special names. The most constant of these (fig. 76) are two in front of the eye, a **prefrontal** which joins the antero-lateral angle of the frontal, and a more lateral **lacrimal bone,** connected in many forms with the opening of the lacrimal duct. The orbit is similarly bounded behind by a more medial **postfrontal** and a more lateral **postorbital** bone, the latter extending to the zygomatic. Occasionally **supraorbitals** intervene between the frontal and the orbit while there may be a similar chain of **infraorbitals** between the orbit and the maxilla-zygomatic bar. Last to be

mentioned of the cranial membrane bones are a pair of **septomaxil-laries** (fig. 77) which lie in the floor of the nasal cavities. Their relations are very uncertain. They occur in all living groups of Amphibia, in *Sphenodon* and many Theromorphs and lizards, and have been found in at least one genus (*Tatusia*) of mammals.
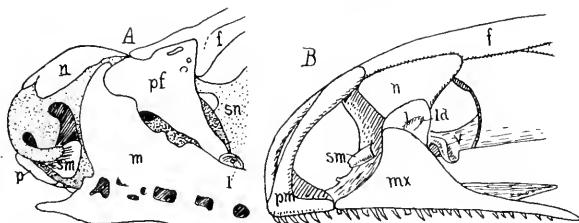
FIG. 77.—Nasal region of (*A*) 47 mm. *Lacerta agilis* (Gaupp, '10) and (*B*) *Ranodon olympicus* (Noble, '21). Cartilage stippled. *f*, frontal; *l*, lacrimal; *ld*, groove for lacrimal duct; *m*, maxilla; *p, pm*, premaxilla; *pf*, prefrontal; *sm*, septomaxillary; *v*, vomer. (Gaupp's interpretations modified.)

The whole dorsal side of the primitive cranium, as shown by many fishes, Stegocephals (fig. 76) and many Theromorphs (Cotylosaurs. fig. 78) is covered by bone, the only gaps, aside from the parietal
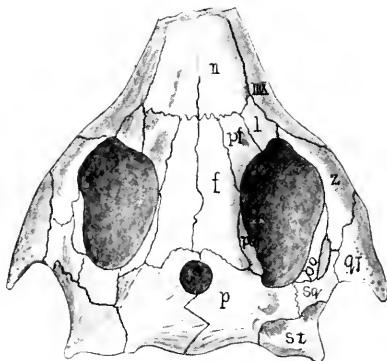
FIG. 78.—Cranium of *Procolophon* (Seeley, '88); *f*, frontal; *l*, lacrimal; *mx*, maxilla; *n*, nasal; *p*, parietal; *pf*, prefrontal; *po*, postorbital; *pof*, postfrontal; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal; *z*, zygomatic.

foramen, being the nares and orbits (**stegocrotaphic skull**). In other groups there are usually gaps (**fossæ**) between certain of the bones. Occasionally some of these lie in front of the orbits (**antorbital vacuities**) and are of little morphological importance. Those behind the orbits are separated from each other and from the margin of the cranium by bars (**arcades**) of bone. At most there are three of these

postorbital fossæ. The more lateral of these, the **infratemporal fossa,** is usually bounded on the lateral side by an arcade of squamosal, quadratojugal and zygomatic (when the quadratojugal is absent, by the other two). On the medial side an arcade of squamosal and postorbital or postfrontal, separates this fossa from the **supratemporal fossa,** which is limited medially by parietal and frontal bones. The third, the **post-temporal fossa,** lies between parietal, supratemporal and occipital bones, the opisthotic and squamosal sometimes entering its boundaries. Occasionally but one of these fossæ may be present. On the other hand supra- and
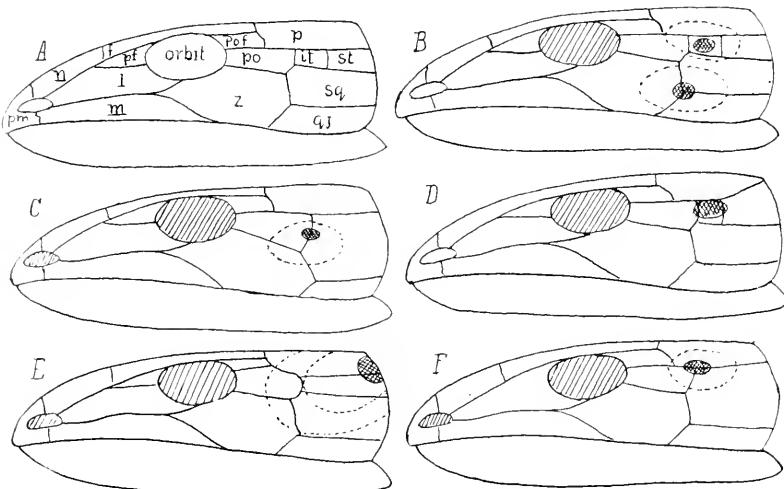
Fig. 79.—Schema of the formation of vacuities (cross-lined) and arcades in Reptilia (Versluys, '19). *A*, primitive reptile; *B*, diapsid type; *C*, first synapsid type (Theromorphs); *D*, second synapsid type, (Sauropterygia and Placodonta); *E*, Chelonia; *F*, Ichthyosaurs. The dotted lines, extent of later vacuities. *f*, frontal; *it*, intertemporal; *l*, lacrimal; *m*, maxilla; *p*, parietal; *pf*, prefrontal; *pm*, premaxilla; *po*, postorbital; *pof*, postfrontal; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal; *z*, zygomatic.

infratemporal fossæ may unite (**temporal fossa**) by interruption of the upper arcade. Lastly the lower arcade may break, leaving the temporal fossa incomplete, while by interruption of the postorbital bar (postfrontal, postorbital, zygomatic) orbit and temporal fossa are confluent.

The origin and relations of these fossæ have had various explanations, and more than one classification of Tetrapoda has been based upon them. One of these views is illustrated in figure 79. Another view has given some useful terms, as by it groups with but a single (the superior) fossa are known as **Synapsidans,** those with both upper and lower fossæ are **Diapsidans.**

Another series of membrane bones, arising primarily by the fusion of the bases of teeth, occurs in the roof of the mouth (cranial floor); maxilla and premaxilla belonging to this group. In many lower Gnathostomes the middle part of the oral roof is formed by a **parasphenoid bone** (fig. 80) which lies just ventral to basi- and presphenoid cartilages, its extent and development being inversely reciprocal with that of the cartilage sphenoid bones. In the higher classes it is reduced or absent.[1] When true jaws are developed, the pterygoquadrate bars no longer meet in the middle line, but may join the sides of the cranium or end freely. Usually in Tetrapoda a large part of the pterygoid cartilage does not ossify, but is overlaid with a membrane bone which is called the **pterygoid.** (This whole matter of pterygoid homology needs a thorough review.) The pterygoid bars and their associated membrane bones are continued medially and ventral to the cranium by a **palatine bone** on either side, the palatines of the two sides often meeting in the middle line. Between these (dermo) palatines and the premaxillæ is a somewhat similar pair of **vomers** (unpaired in Teleosts) lying in front of and between the primitive choanæ. Parasphenoid, palatines and vomers frequently bear teeth, an indication of their origin (p. 7).

FIG. 80.—Palatal surface of *Acanthostoma* (Stegocephal, Jaekel, '06). *mx*, maxilla; *o*, orbit; *pa*, palatine; *pmx*, premaxilla; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *t*, transversum; *v*, vomer.

The membrane bones of the visceral arches include those of the oral roof, the margins of the upper jaw and nearly all of the bones of the lower jaw, but dermal bones are practically absent from hyoid and branchial arches. Those of the lower jaw are arranged around Meckel's cartilage which usually disappears, but may persist inside them through life. The extreme of separate bones in the mandible includes the following on either side of the jaw: A **dentale** (**dentary**) in front, which, near the tip of the jaw, surrounds the Meckelian and extends farther back on its outer than on its inner side. This is

[1] It has been suggested recently that the parasphenoid is the homologue of the mammalian vomer, necessitating a new name (**prevomer**) for the so-called vomers of the non-mammalian Vertebrates. So far there is little developmental support for this view, and until better evidence appears it is better to retain the older view and names.

followed on the medial side by one or more splint-like bones, the **splenials** (**operculare**) which, with the dentalia, are the only tooth bearing bones in the lower jaw. On the lower margin of the jaw, and extending up on either side and reaching back almost to the angle of the jaw, is an **angulare** with a **sur(supra)angulare** dorsal to it. At the point where most of the occludent jaw muscles are attached a **coronoid** (**complementare**) **bone** is developed (and in Teleosts a '**sesamoid articulare**' may appear at the insertion of the muscles). On the medial and ventral side of the posterior part of the Meckelian and the articulare is a **goniale** (**derm-** or **autarticulare**) which usually fuses with the articulare. Of all of these membrane bones of the lower jaw, dentale, angulare and splenial are the most constant as separate elements.
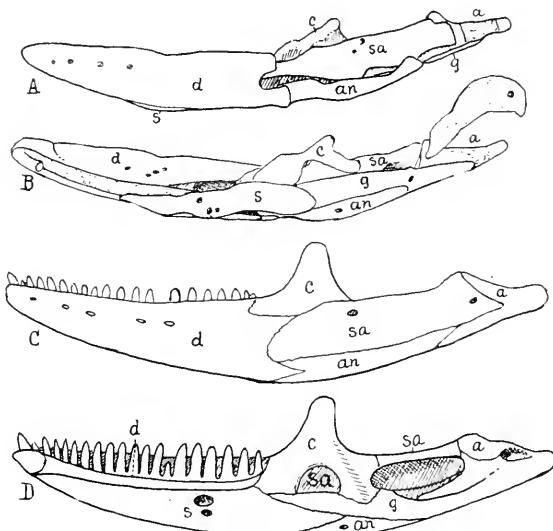
FIG. 81.—Lower jaw of *Lacerta* (Gaupp, '11). *A*, outer and *B*, inner side of jaw of 47 mm. embryo; *C*, outer and *D*, inner side of adult jaw. *a*, articulare; *an*, angulare; *c*, coronoid; *d*, dentale; *g*, goniale; *q*, quadrate; *s*, splenial; *sa*, surangulare.

THE SKULL IN SEPARATE CLASSES

CYCLOSTOMATA.—The Cyclostome skull never passes the cartilage stage, but several kinds of cartilage—true and pseudo, hard and soft—are described in it. The skulls are peculiar and many parts are not readily homologised with those of other Vertebrates, and there is difficulty in comparing all details of Myxinoid and Petro-myzontid skulls.

Parts of the early skull of the *Ammocœtes* stage of *Petromyzon* (fig. 82) are comparable with those of Gnathostomes. The notochord extends forwards to the hypophysial region and is flanked by parachordal plates which fuse later with the otic capsules. A trabecula on either side extends lateral to hypophysis and infundibulum, the two trabeculæ uniting in front in the equivalent of an ethmoid plate, and enclosing a fenestra hypophyseos. A slender bar passes obliquely forwards and laterally from the parachordal, in front of the otic capsule. This has been called both a quadrate and a hyoid, but is certainly neither.

The same parts are recognizable in the skull of the Adult lamprey (fig. 83). Parachordals and chorda form a basal plate, limited laterally by the otic capsules and in front by the fossa hypophyseos which is bounded laterally by the trabeculæ. Farther forwards is a broad ethmoid plate below the olfactory organ. The roof of the brain case is largely membranous, but there is a synotic tectum connecting the otic capsules of the two sides. The single median nasal capsule is attached to the rest of the cranium by ligaments. Beyond this, comparisons with other skulls are uncertain.

FIG. 82.—Chondrocranium of larval (Ammocœte) lamprey (Schneider, '02). *h*, "hyoid;" *nc*, notochord; *oc*, otic capsule; *pa*, parachordal; *tr*, trabecula.

Anterior to the ethmoid region is a 'posterior median dorsal cartilagen flanked by 'lateral cartilages' and continued forwards by an 'anterior media,' dorsal cartilage,' these supporting the buccal cavity in front of the median naris. These cartilages support an annular 'labial cartilage' with a 'styliform cartilage' on either side. Lateral to the trabecula is a subocular bar which has a part terminating in a 'styloid process' and connected with the branchial basket. This basket is composed of a connected and fenestrated cartilage surrounding the gill region and enclosing also the pericardium. It consists of four longitudinal bars (hypochordal, epitrematic, hypotrematic and ventral) connected by vertical bars between each two gill-clefts. The so-called tongue contains a series of large lingual (basal) cartilages to which the muscles of this rasping organ are attached.

In the Myxinoid skull (fig. 84) parachordals, otic and nasal capsules, trabeculæ and subocular bar are easily made out, but other homologies are difficult. The cranial roof is membranous, the median nasal capsule is fenestrated and the nasal duct, leading back from the naris, is supported by a series of cartilage rings. Four pairs of cartilages support the tentacles. The branchial skeleton is less complete than in Petromyzontes, there being two or three bars in the anterior

FIG. 83.—Ventral and lateral views of skull of lamprey *Petromyzon* (Parker). *ad*, anterior dorsal cartilage; *bb*, branchial basket; *gc*, gill clefts; *lc*, labial cartilage; *ldm*, lateral distal mandibular; *lg*, lingual cartilage; *nc*, nasal capsule; *oc*, otic capsule; *on*, optic nerve; *pc*, pericardial cartilage; *pd*, posterior dorsal cartilage.
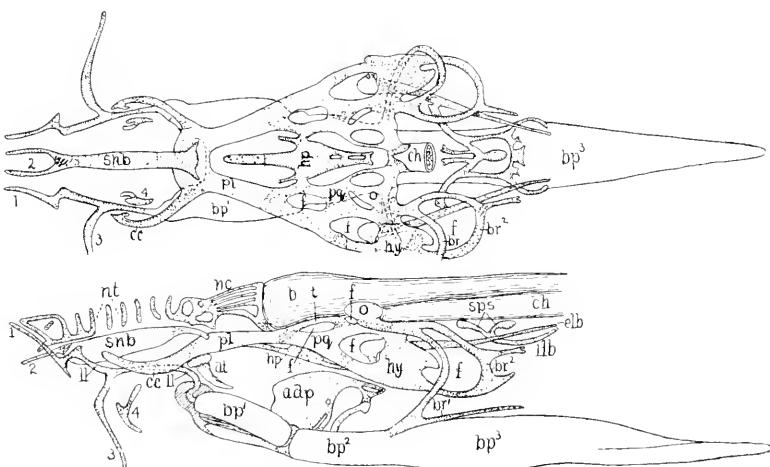
FIG. 84.—Dorsal and lateral views of skull of Myxine (Cole, '05); fine stippling, soft cartilage; coarse stippling hard cartilage; white, hard pseudocartilage; cross-lined, soft pseudocartilage; *adp*, anterior arch of dental plate; *b*, brain; *bp*, basal plates of lingual apparatus; *br*, branchial arches; *cc*, cornual cartilages; *ch*, notochord; *dt*, median dorsal tooth; *elp*, external lateral velar bar; *f*, fenestra; *hp*, hypophysial plate; *hy*, 'hyoid' arch; *ilp*, internal lateral velar bar; *ll*, lateral labial; *nc*, nasal capsule; *nt*, cartilages of nasal tube; *o*, otic capsule; *pl*, 'palatine' bar; *pq*, 'pterygoquadrate;' *snb*, subnasal bar; *sps*, suprapharyngeal skeleton; *t*, "trabecula;" 1-4, tentacular cartilages.

part of the pharyngeal wall, two of which are connected with the styloid process, the other (so-called hyoid) extends to the lingual series. Besides these there are vestigial cartilages at the openings of the gill-clefts and œsophageocutaneous duct in *Bdellostoma*. The lingual cartilages are three, the anterior segment consisting of two elements, the others being single.

Attempts have been made to homologise the parts of the Cyclostome skull with those of Gnathostomes, but, with the exception of the points made above, few comparisons are convincing. The subocular bar has been compared with the pterygoquadrate, but the branches of the fifth nerve pass below it. The styloid process has more resemblance to the hyoid. There is evidence that the branchial basket differs from that of Gnathostomes as it is somatic rather than splanchnic (p. 66) and in *Petromyzon* the ventral aorta lies within, rather than ventral to the median ventral bar. It has also been argued that the lingual cartilages are really the lower jaw structures of Gnathostomes and that the distinction between the jawed Vertebrates and Cyclostomes does not hold. But the evidence for this is weak and needs considerable additional support.

Palæospondylus.—At the anterior end of this problematic fossil is a structure naturally regarded as a skull (fig. 85), but concerning its parts there is much divergence of opinion. It has recently been studied by means of sections, with the following results: The cranial capsule is open above, below and in front, and is connected on either side with the cavity of the otic capsule which, as in Cyclostomes, has two semi-circular canals. In front there are dorsal and ventral bars (rostralia), the latter connected by a transverse bar (ampyx). behind which is a part of the cranial floor (tauidion) and probably nasal capsules. Below there are four branchial arches which are close, laterally, on either side to an angular bar (gammation) in front of which is a pregammation. Gammation and pregammation are possibly hyoid and mandibular arches. Connected with the last branchial arch on either side is a postbranchial plate. Sections show no traces of ribs or appendages.
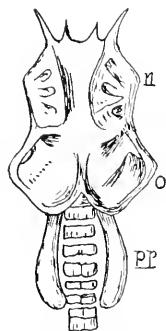
FIG. 85.—Head of *Palæospondylus* (Traquair). *n*, nasal capsule; *o*, otic capsule; *pp*, post branchial plates.

ELASMOBRANCHII.—In all Elasmobranchs the cranium is a continuous cartilage without separation into discrete parts, but with large openings (**fontanelles**) and smaller foramina for nerves and vessels. Except in Holocephali the visceral skeleton is connected to the cranium only by ligaments or is articulated with it, the two parts never fusing. In adults, especially of the larger species, it is calcified on the outer surface, but bone is never developed.

There are several separate parts in early development (fig. 86). Notochord and parachordals, as elsewhere, form a basal plate extending laterally beneath the otic vesicles. The head is flexed just in

6

front of the basal plate, hence the trabeculæ (morphologically ventral to the brain) are directed downwards, instead of being horizontal as in the general statement above (p. 59), and in Amphibia. Dorsal to and at some distance from the trabecula is a second cartilage, the sphenolateral (pleurosphenoid, alisphenoid), nerves II to V passing between trabecula and sphenolateral, while nerves VI and VII are dorsal to the trabecula and posterior to the hinder end of the upper cartilage. The otic capsule begins as an elevation of the dorsal side of the basal plate, gradually extends dorsally and then medially so that the otic vesicle becomes enclosed in cartilage, except on the medial side where openings for nerves and for ducts (endo- and peri-lymph) remain open permanently. There is no fenestra on the
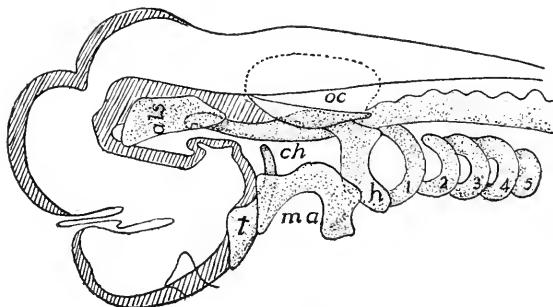
Fig. 86.—Early chondrocranium of *Acanthias* (Sewertzow, '99). The brain in outline. *als*, sphenolateral; *ch*, anterior part of notochord; *h*, hyoid arch; *ma*, mandibular arch, not yet divided; *oc*, otic vesicle; *t*, trabecula; 1–5, branchial arches. (Compare with fig. 65.)

external surface at any time. The posterior part of the basal plate is formed by rudiments of occipital vertebræ (p. 62), the number of which varies, according to author and species, from four to seven.

Later these vertebræ form neural arches, the first joining the posterior cupula of the otic capsule, leaving the jugular foramen between the two, while between the more posterior arches (which fuse) are similar foramina for the spino-occipital nerves. These arches meet dorsally and, with upgrowths from the otic capsules, form the synotic tectum which is perforated for the external openings of the peri- and endolymph ducts.

Each trabecula fuses with the basal plate in front of the otic capsule, and a little later the anterior trabecular ends unite to form the ethmoid plate, enclosing the hypophysis in a large hypophysial fenestra. Trabecula and sphenolateral plate become united by

cartilage growths, to a plate in which ali- and orbitosphenoid parts are distinguishable only by nerve exits, the arrangement of which differs in different genera, but that of the second nerve indicates approximately the posterior limit of the orbitosphenoid. The prootic fissure behind the alisphenoid region contains the fifth and seventh nerves, and is later converted into the foramen lacerum by the extension of the sphenolateral back to the otic capsule.
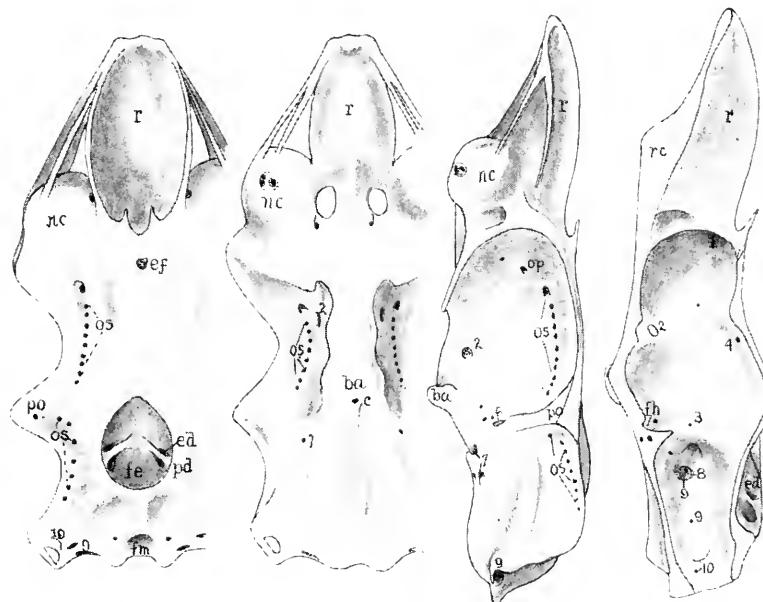
FIG. 87.—Dorsal, ventral, lateral and sectional views of cranium of *Acanthias* (Wells, '17). *bs*, basilar process; *c*, carotid foramen; *ed*, opening of endolymph duct; *ef*, epiphysial foramen; *fe*, endolymph fossa; *fh*, fossa hypophyseos; *fm*, foramen magnum; *nc*, nasal capsule; *op*, foramen for ophthalmicus profundus; *os*, for branches of ophth. superficialis; *pd*, for perilymph duct; *r*, rostrum; *rc*, rostral carina; 2–10, nerve exits.

A separate cartilage arises near the anterior end of the orbitosphenoid on the outer side and soon joins the cranial wall, forming the **antorbital process** which separates the orbit from the nasal capsule. The upper borders of the interorbital cranial walls extend dorsally and medially and form the roof of the anterior part of the cranial cavity, extending back to the synotic tectum, but leaving a large gap, the **anterior fontanelle,** in front. These side walls also grow forwards, forming the medial walls of the nasal capsule and the large anterior projection (**rostrum**) of the cranium. The cranial floor is completed in the same way, the medial growths joining the

ethmoid and basal plates and closing the sella turcica in the middle line.

The visceral arches are continuous bars at first (fig. 86), separating later into the parts (Fig. 71) of the adult, and still later becoming connected by copulæ in the mid-ventral line. The halves of the pterygoquadrate also fuse in front. The labials are late in appearing and branchial rays arise independently of the arches.
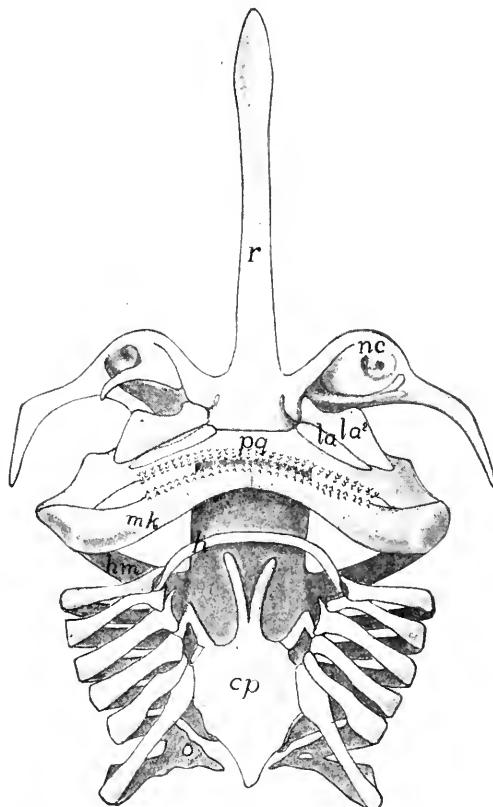
FIG. 88.—Ventral side of skull of skate (Gegenbaur, '72). *cp*, copula; *h*, hyoid; *hm*, hyomandibular; *mk*, Meckelian; *nc*, nasal capsule; *pq*, pterygoquadrate; *r*, rostrum.

The adult has lost the characteristic flexure of the young, only traces of it remaining in the sharp angle of the dorsum sellæ and the marked basal angle on the ventral surface (fig. 87). The floor is complete, as is the roof as far forwards as the level of the nasal capsules, in front of which cartilage is replaced by membrane, easily torn away, leaving the large anterior fontanelle which extends to the

tip of the rostrum, the anterior extension of the cranium. This rostrum varies in form, sometimes being spoon-shaped, or by fenestration of this, consisting of three bars which converge forwards. It is sometimes so short as to be practically absent, but in skates (fig. 88) it is very long, and in sawfishes extends most of the length of the 'saw.'

The parietal organ lies in a foramen, either in the membrane of the fontanelle or in the cartilage a little farther back (fig. 87, *cf*). The nasal capsules, with the nares on the ventral side, are joined to the side cranial walls and open widely (**olfactory foramina**) to the brain case. The orbits are bounded in front and behind by **pre-** and **postorbital crests** which are connected dorsally by a strong **supraorbital crest,** the line between this and the wall of the brain case being indicated on the dorsal surface by a row of foramina for branches of the superficial ophthalmic nerve (fig. 87, *os*). Some Elasmobranchs have a narrower **suborbital crest,** but this is usually lacking, the orbits of the two sides being separated ventrally by a median infraorbital ridge which usually bears near its middle on either side a **palatobasal articular surface** (*ba*) over which the palatal process of the lower jaw plays. The wall of the orbit is perforated by vascular and nerve foramina, the position of which varies with the genus. It also has connected with it a cartilage **optic pedicel** which supports the eyeball.

The otic capsules are less prominent than in the embryo. Ridges on the surface of each show the position of the semicircular canals. In the cranial roof between the capsules is a more or less developed **endolymph** (**parietal**) **fossa,** in which are the openings of the endo- and perilymph ducts. The base of the cranium has foramina for the exit of ninth and tenth nerves, the foramen magnum and smaller openings for the spino-occipital nerves, the number of which varies with the number of vertebræ included in the cranium. In skates and Holocephali the foramen magnum is bounded laterally by occipital condyles for articulation with the first vertebra, but in sharks the skull is immovably united with the spinal column. In *Carcharias* the occipital region extends over the anterior vertebræ.

Most Elasmobranchs have seven visceral arches—mandibular, hyoid and five branchial—but in Notidanids there are six (*Hexanchus* and *Chlamydoselachus*—the latter sometimes with remnants of a seventh) or seven (*Heptanchus*, fig. 69) gill arches. Most of the gill

arches are posterior to the cranium and are not connected with it, but some or all may be attached to the anterior vertebræ in skates. The anterior branchial arches are most complete, there being a tendency to reduction, modification, and fusion in the posterior. Each arch typically has four elements (p. 65), the two halves of each arch being connected by a basibranchial, but it is uncertain with whether, morphologically, these copulæ lie between or alternate the arches. Very frequently the successive copulæ fuse to a larger plate, and the last of the series may be very large, and, when lying just ventral to the heart, is called a **cardiobranchial cartilage** (fig.

69, *A*, *C*). Each arch supports a number of cartilage branchial rays which extend from epi- and ceratobranchials as supports into the branchial septum. Usually filiform, they are sometimes branched or plate-like, and are most numerous in skates. A number of Elasmobranchs have **extrabranchial cartilages,** above and below, and farther out in the septum than the arch, which form an additional support for the septum (fig. 89)

FIG. 89.—Branchial arch of *Heterodontus* (Daniel, 15). *br,* branchial rays; *cb,* ceratobranchial; *eb,* epibranchial; *ex,* extrabranchials; *pb,* pharyngobranchial.

The modifications of the hyoid arch are important. Notidanids (fig. 93) are most primitive, the hyomandibula being small, resting against the otic capsule and articulating ventrally with the hyale only, its connexion with the mandibular arch being only by ligament. Most Elasmobranchs have the ventral end of the hyomandibula larger and articulating with, not only the ceratohyoid, but with the mandibular arch as well, thus forming part of the suspensor of the jaws. This reaches its extreme in *Torpedo.* In Raiæ (fig. 88) the hyomandibula is purely suspensorial, the hyale being separate from it and articulating directly with the otic region. Hyomandibula and ceratohyal bear gill rays. The hypohyals of the two sides are connected by a basihyal which often has an anterior lingual process, sometimes interpreted as indicating a former copular connexion of mandibular and hyoid arches, similar to the connexion of hyoid and branchial arches in some species.

The mandibular arch (pterygoquadrate and Meckelian cartilages) forms the functional upper and lower jaws, each with teeth, usually

confined to the margins, but in a few forms (feeding on hard-shelled animals) extending some distance in the mouth. The attachment of the pterygoquadrate to the cranium varies in different groups. Notidanids have a strong process (especially strong in *Heptanchus*, fig. 90) on the upper margin of the pterygoquadrate which articulates with the side of the postorbital crest, and in addition this element is connected by ligaments with the hyoid arch and thus indirectly with the cranium (amphistyly). In most species the pterygoquadrate is connected in front with the cranium by ligaments, while behind, the anterior angle of the hyomandibula intervenes
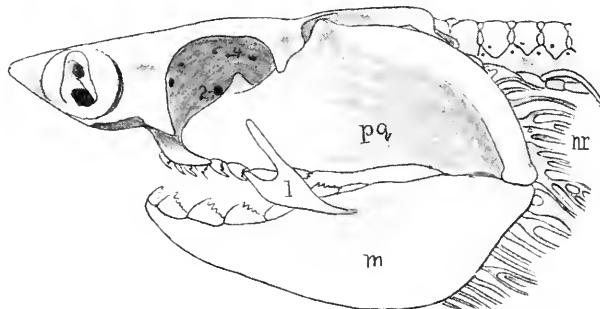
Fig. 90.—Skull of *Heptanchus maculatus* (Daniel, '16). *hr*, hyoid rays; *m*, Meckel's cartilage (lower jaw); *pq*, pterygoquadrate; 2–4, nerve exits.

between cranium and upper jaw (hyostyly), this reaching its extreme in skates where the hyomandibula is wholly suspensorial. Each half of the pterygoquadrate may have a **palatal process** on its upper margin which slides on the palatobasal surface (p. 85) of the cranium, tending to prevent disarticulation of the jaws by the struggles of the prey. In skates the suspension of the jaws is wholly hyomandibular, the anterior ligaments being lost, thus allowing the protrusion of the jaws in seizing food.

The Holocephali differ from all other sharks in the attachment of the jaws. In the young the pterygoquadrate is free from the cranium, but fuses early with its wall (fig. 91, *B*) so completely that no trace of a suture persists in the adult. This autostyly is strikingly similar to conditions in higher groups.

Sharks have from one to three spiracular cartilages (supporting the spiracular gill) between the hinder end of the pterygoquadrate and the hyoid. These are sometimes regarded as remnants of a lost visceral arch. These cartilages in skates are more closely related to the anterior side of the mandible.

Labial cartilages occur in most sharks, though lacking in some and reduced in skates. Nothing need be added to the statements on p. 68. Meckel's cartilage (lower jaw) calls for but slight notice. It is articulated to the hinder end of the pterygoquadrate and is capable of motion through a large arc in opening and closing the mouth.

In correlation with the great development of the pectoral fins and their connexion with the tip of the head, the cranium of Raiæ has several modifications. Some have the rostrum enormously developed (fig. 88), and in sawfishes (Pristidæ) it extends far forwards, its lateral margins bearing denticles or larger teeth. In skates the
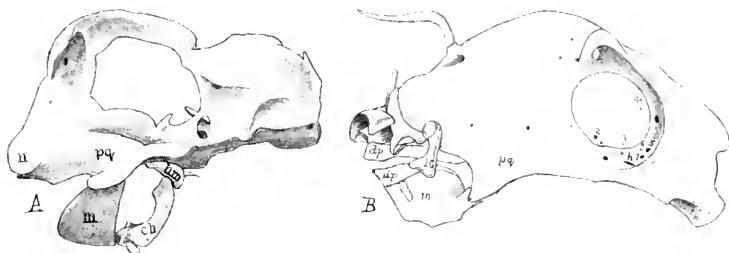
FIG. 91.—Skulls of (A) embryo (45 mm. long) *Chimæra* (Dean, '06) and *B*, adult *Chimæra* (Allis, '17). *ch*, ceratohyal; *dp*, dental plates; *lc*, labial cartilages; *hm*, hyomandibular; *m*, Meckelian; *n*, nasal capsule; *pq*, pterygoquadrate.

anterior angle of the pectoral fin is connected with the head by an **axial process,** arising in line with the propterygium, and usually articulated with the preorbital crest. In *Trygon*, where the rostrum is short, the axial processes of the two sides extend beyond the head. *Torpedo* has two rostral bars, the middle of the usual three having been lost. Most skates have lost the primary flexure of the head, and lack basal angle and dorsum sellæ (p. 70), and the hypophysial fossa has been obliterated. Labial cartilages are poorly developed in skates.

HOLOCEPHALA.—These sharks (often called ratfish) differ from other Elasmobranchs in being autostylic. They have three rostral cartilages (fig. 92), the middle being at a higher level than the others. The short, strong jaws support the large dental plates. No hyomandibula is evident in the adult, but it is not decided whether it be fused with the otic region or absorbed in the quadrate part of the pterygoquadrate. The rest of the hyoid arch is peculiar in having

small epi- and pharyngohyals, dorsal to the ceratohyal.   The inter-
orbital septum is membranous and the brain cavity is restricted to
the postorbital part of the cranium.   There are no fontanelles.   The
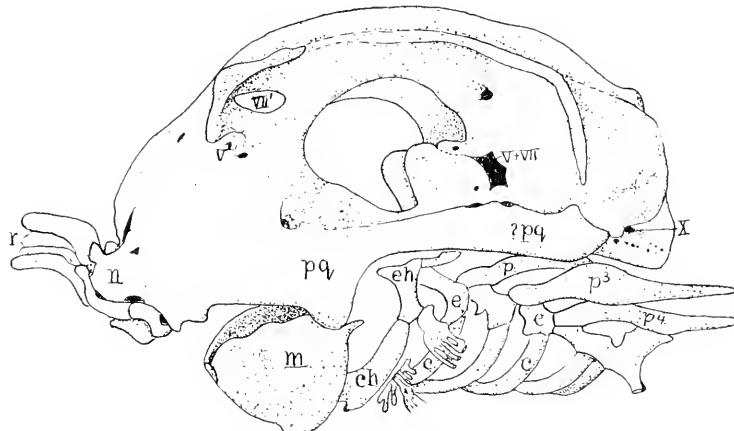
FIG. 92.—Chondrocranium of embryo *Callorhynchus* (Schauinsland, '03). *c*,
ceratobranchials; *ch*, ceratohyoid; *e*, epibranchial; *eh*, epihyal; *m*, Meckel's cartilage;
n, nasal capsule; *p*, pharyngobranchial; *pq*, pterygoquadrate (uncertain if posterior
part be such); *r*, rostral cartilages; *V-X*, nerve exits.

otic capsules open widely to the cranial cavity and the skull is mov-
ably articulated to the spinal column by an occipital condyle.
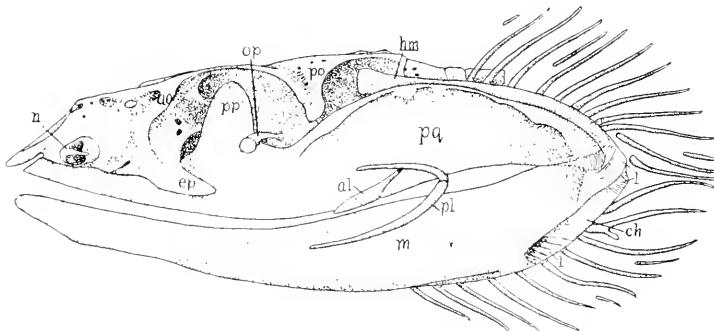
FIG. 93.—Skull of *Chlamydoselachus* (Allis, '23).   *al*, anterior labial; *ao*, antorbital;
ch, ceratohyal; *ep*, ectethmoid process; *hm*, hyomandibula; *l*, ligaments; *m*, mandible;
n, narial cartilage; *op*, optic pedicel; *po*, postorbital process; *pl*, posterior labial; *pp*,
palatal process of *pq*, pterygoquadrate.

Some other features of Elasmobranch skulls are assembled here.
A few genera (*Chlamydoselachus*, fig. 93, *Centrobatis*, etc.) have the
rostrum reduced so that the mouth is nearly terminal.   The former

genus differs from other Notidanids in not being amphistylic, the otic process not reaching the cranium. *Pliotrema* (So. Africa, near *Acanthias*) differs from its relatives in having six branchial arches. A few fossil genera of Squali (*Edestus, Helicoprion*) have the lower jaw greatly elongate and spirally coiled, the coils armed with large teeth of problematic use.

Few details are known of several groups of fossil Elasmobranchs. Three of them (Ichthyotomi, Cladoselachii and Acanthodii) are amphistylic like Notidanids. Most have five gill-clefts with corresponding arches (some Cladoselachii may have had six or seven) which are divided into four parts, the pharyngobranchial possibly being absent. The rostrum is small and the mouth nearly terminal. No bone is developed, but the cartilage was sometimes calcified.

OSTRACODERMA.—The oldest and least understood Vertebrates grouped under this head had an anterior region ('head') which in the simplest forms
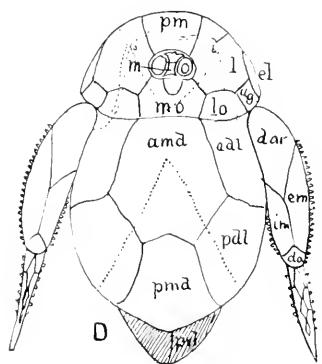
FIG. '94.　　　　　　　　　　　　　FIG. 95.

FIG. 94.—Dorsal and ventral restorations of *Bothriolepis canadensis* (Traquair, '04). *adl*, antero-dorsolateral plate; *ag*, angular; *amd*, anterior median dorsal; *avl*, antero-ventrolateral; *c*, centrals of lower appendage; *da*, dorsal anconeal; *dar*, dorsal articular; *el*, extralateral; *em*, external marginal; *im*, internal marginal; *l*, lateral; *lo*, lateral occipital; *m*, median; *mi*, marginals of lower appendage; *mo*, median occipital; *mv*, median ventral; *mx*, maxillary plate; *o*, ocular; *pdl*, posterior dorsolateral; *pm*, premedian; *pmd*, posterior mediodorsal; *pvl*, posterior ventrolateral; *sl*, semilunar; *va*, ventral anconeal; *var*, ventral articular.

FIG. 95.—Dorsal side of head of *Pteraspis* (Lankester, '68).

(*Lanarkia, Thelodus*) is covered by numerous irregularly arranged scales, apparently placoid. Others have the scales united in plates (not true bone) and others the whole head is enveloped in such an armor (figs. 94, 95). It is impossible, at present, satisfactorily to homologise these plates with the bones of the normal ossified skull, but there is an approach to the cranium of higher
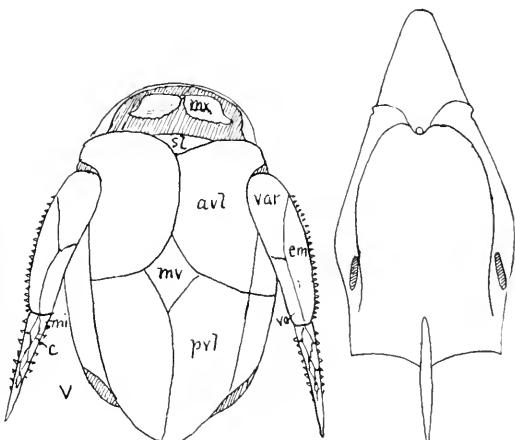
vertebrates and an advance beyond the purely cartilage skull of Elasmobranchs. A few figures with the usual nomenclature of parts are as good as any detailed description for present purposes. Ostracoderms are often distributed into groups of Heterostraci, Osteostraci and Antiarcha; the relations of all to other Vertebrates being very uncertain.

TELEOSTOMI are normal fishes, higher than Elasmobranchs, in which membrane bones, and to a greater or less extent, cartilage bones have developed in the skull. The Chondrostei, except for
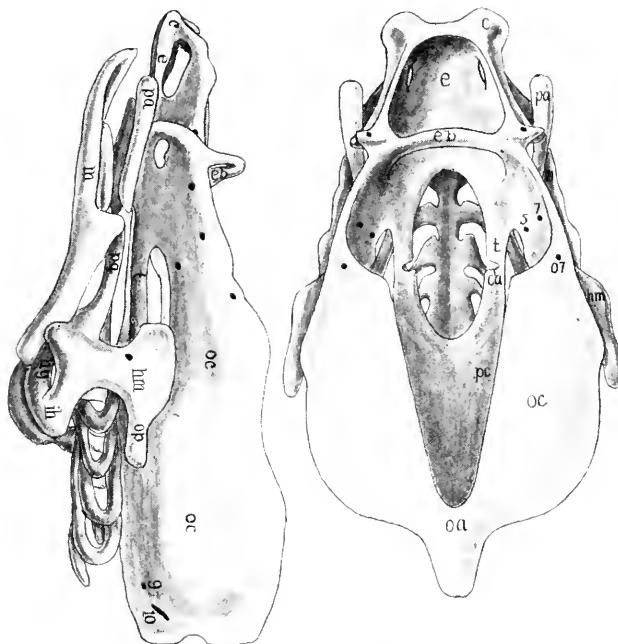
Fig. 96.—Dorsal and side views of *Amiurus* chondrocranium (Kindred, '19). *c*, ethmoid cornu; *ca*, notch for carotid; *e*, ethmoid plate; *eb*, epiphysial bar; *hm*, hyomandibula with foramen for hyomandibular nerve; *hy*, hyale; *ih*, interhyal region; *m*, Meckel's cartilage; *oa*, occipital arch; *oc*, otic capsule; *op*, opercular process; *pa*, 'palatine' cartilage; *pc*, parachordal; *pq*, pterygoquadrate; *t*, trabecula.

bones, have hardly passed the sharks, and the following general statement omits them, discussion of their features being given later. Except for a few (mostly lower) forms, little is known of the development of the skull and the homologies of several of the bones are uncertain. To a greater extent than elsewhere, certain bones have a double origin, being formed by an intimate union of a cartilage bone with an overlying bone, clearly of dermal origin, as occurs in the

union of pterotic and squamosal, sphenotic and postfrontal, dermal ethmoid with mesethmoid, etc.

The chondrocranium (fig. 96) is usually well developed and a large part of the cartilage persists in the adult. In the lower groups (Ganoids and most Physostomi) the cranial cavity extends into the ethmoid region (platybasic skulls). In others (tropibasic) the cranium is constricted between the orbits and an interorbital septum (permanently cartilage or ossifying later) usually occurs, the brain being restricted to the postorbital part of the cranium (fig. 97).
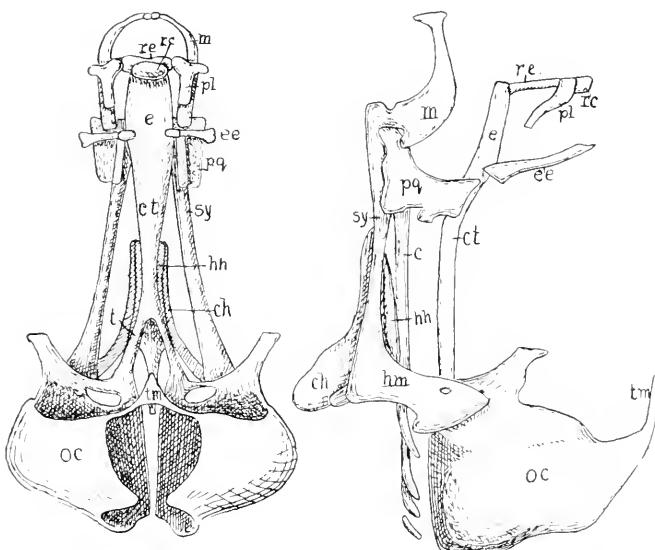
FIG. 97.—Dorsal and side views of chondrocranium of *Syngnathus fuscus* (Kindred, '21). *c*, copula communis; *ch*, ceratohyoid; *ct*, common trabecula; *e*, ethmoid plate; *ee*, ectethmoid; *hh*, hypohyal; *hm*, hyomandibula; *m*, Meckelian; *oc*, otic capsule; *pl*, palatine; *pq*, pterygoquadrate; *re*, rostral process of ethmoid; *sy*, symplectic; *t*, trabecula; *tm*, median tectum.

As there are numerous roofing bones, the chondrocranial tegmen is usually more incomplete than in Elasmobranchs, but the synotic tectum usually persists, and not infrequently parts of the cartilage roof are retained farther forwards, forming a transverse bar or plate in the epiphysial region (fig. 96). Most Teleostomes have the cartilaginous otic capsules widely open to the brain chamber.

The following ossifications of the chondrocranium are the more usual, but some of these are lacking here and there. In the base

of the cranium (fig. 98) are the four occipitals, the supraoccipital
being the least constant, and when present, it may be excluded from
the margin of the foramen magnum by the meeting of the exoccip-
itals above the opening. The supraoccipital usually develops a
strong (occipital) spine, pointing backwards, in response to the
strain of the large dorsal trunk muscles.
The cranial floor largely persists as car-
tilage, there being a large parasphenoid
below it, but sometimes there is a small
basisphenoid behind the hypophysis.
More constant, and extending up in the
side walls of the skull are the ali- and
orbitosphenoids of either side, these
being well developed in platybasic fishes,
but are reduced (especially the orbito-
sphenoid—lacking in many Acantho-
pteri) where an interorbital septum
occurs.

Otic bones are more numerous in
most Teleostomes than in higher

FIG. 98.—Base of cranium of
Pleuronectes (Cole and Johnstone,
'02). *eo*, exoccipital; *epo*, epiotic;
op, opisthotic; *pto*, pterotic; *so*,
supraoccipital.

Vertebrates. When best developed, an opisthotic (very variable,
sometimes several, sometimes lacking) ossifies in the posterior cupula.
The prootic, in the floor and anterior wall, extends into the orbital
region, the fifth nerve passing in front of or through its anterior part.
The sphenotic, usually closely associated with the overlying post-
frontal, arises in the anterior cupula, and on the posterior outer
surface of the capsule is a compound squamoso-pterotic, its two
elements distinct in the early stages. In the angle between supra-
and exoccipital, and pterotic there may be an epiotic (**paroccipital**)
forming the postero-lateral angle of the cranium with which the
supracleithrum of the shoulder girdle articulates.

The dermal bones vary. Usually in the cranial roof are parietals,
frontals and nasals, the bones of each primitive pair frequently
fusing, while parietal and frontal may unite as a fronto-parietal.
The supraoccipital (the interparietal often fused with it) is sometimes
visible behind the parietals, occasionally extending forwards and
separating them. At times the supraoccipital does not ossify and
then the cranium may end with a transverse row of dermal bones,
the middle two of which (**dermoccipitals**) are often called supraoccip-

itals; the lateral members of this row are often called supratem-
porals, but that they are the homologues of the supratemporals of
Tetrapoda is doubtful. All Teleostomes, a few Teleosts excepted,
have the pectoral girdle connected with the cranium by the supra-
cleithrum articulating with the epiotic as mentioned above, and
often with the opisthotic as well, by two heads, the supracleithrum
then appearing as a cranial bone (**posttemporal**). In front, the
cranium may have the mesethmoid cartilage or bone covered by a
derm- or **supraethmoid bone.**
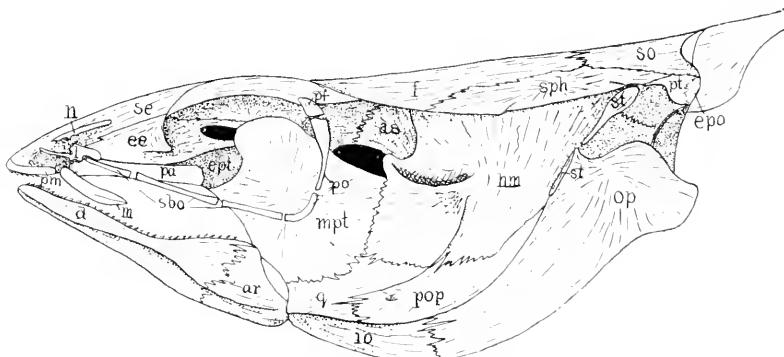
FIG. 99.—Lateral view of skull of *Amiurus* (Kindred, '19). *ar*, articulare; *as*,
alisphenoid; *ee*, ectethmoid; *ept*, epipterygoid; *f*, frontal; *hm*, hyomandibula; *io*, inter-
operculum; *l*, lacrimal; *m*, maxilla; *mpt*, metapterygoid; *n*, nasal; *op*, operculare; *pa*,
palatine; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pop*, preoperculum; *pt*,
pterotic; *q*, quadrate; *sbo*, suboculars; *se*, supraethmoid; *so*, supraoccipital; *sph*, spheno-
tic; *st*, subtemporals.

The lateral line canals nearly surround the eye, and bones may
develop around them (fig. 100), called, according to position, **supra-,**
pre-, post-, and **sub-** or **infraorbitals.** Some of these may be traced
with some certainty in Tetrapoda, and it would appear that the
postorbitals are the homologue of the single postorbital of higher
groups; the anterior and posterior supraorbitals as pre- and post-
frontals, while one of the antorbitals is apparently the lacrimal of
Tetrapoda. It is not so certain that the zygomatic is the equivalent
of the piscine suborbitals.

The roof of the Teleostome mouth (fig. 101) is formed by, in
front, a pair of (frequently toothed) vomers, followed by a long
parasphenoid bone which extends across the floor of the skull and
back to the basioccipital, and may bear teeth, an additional evidence
of its origin (p. 7).

The cartilaginous visceral skeleton is like that of Elasmobranchs. The mandibular arch (pterygoquadrate and Meckelian) early loses its primitive character. Except in Chondrostei the pterygoquadrate does not function as the upper jaw. Its anterior end may rest on the lower side of the ethmoid plate, or the arch may be incomplete here, and its anterior end occasionally is a discrete palatine cartilage (fig. 97). The hinder end of the cartilage is connected with the cranium by a hyomandibular suspensor (is hyostylic) or when the pterygoid rests on the ethmoid plate, is amphistylic. The hyo-
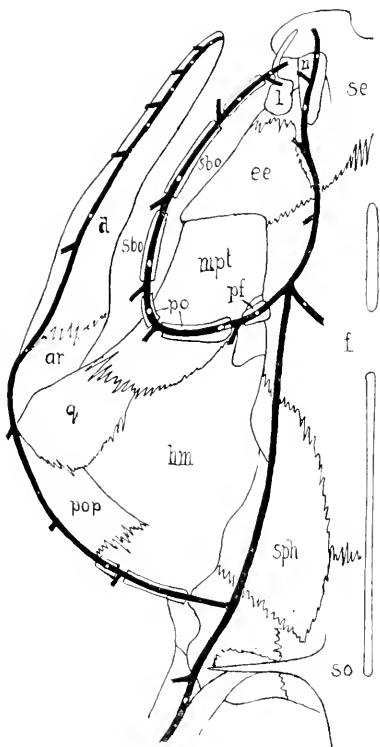
FIG. 100.   FIG. 101.

FIG. 100.—Roofing and lateral bones of skull of *Amiurus*, lower jaw bent laterally (Kindred, '19). *ar*, articulare; *d*, dentale; *ee*, ectethmoid; *f*, frontal; *hm*, hyomandibula; *l*, lacrimal; *mpt*, metapterygoid; *n*, nasal; *pf*, postfrontal; *po*, postorbital; *pop*, preoperculum; *q*, quadrate; *sbo*, suborbitals; *se*, supraethmoid; *so*, supraoccipital; *sph*, sphenotic.

FIG. 101.—Floor of cranium of *Amiurus* (Kindred, '19). *bo*, basioccipital; *ee*, ectethmoid; *eo*, exoccipital; *f*, frontal; *of*, orbital foramen; *os*, orbitosphenoid; *pro*, prootic; *ps*, parasphenoid; *se*, supraethmoid; *sp*, sphenotic; *sqpt*, squamoso-pterotic; *v*, vomer; 2–10, nerve foramina.
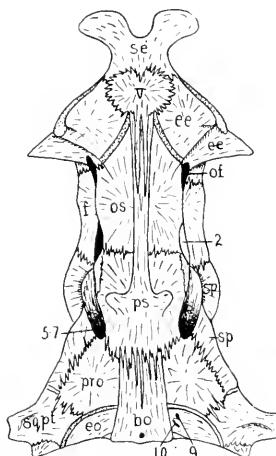
mandibula, usually articulated to the wall of the otic capsule, is generally perforated for the hyomandibular nerve. Its chief ventral connexion is with the quadrate, either directly or with the intervention of a symplectic bone, but there may be a posterior connexion by a distinct **inter-** or **stylohyal cartilage** (fig. 74) with the hyale. The hyale

cartilage is continuous at first, dividing later into cerato- and hypo-hyals, the hypohyals of the two sides being connected by a basihyal copula.

The branchial arches (fig. 102), normally five in number, arise as continuous bars, segmenting later into the separate parts of the adult —usually four (pharyngo-, epi-, cerato- and hypobranchial) in the three anterior arches, each of which is more or less ossified, the dorsal parts of each arch being the most variable. The fourth arch usually lacks the pharyngobranchial; the ceratobranchial is the most con-stant part of the fifth arch.

In all Teleostomes except Chondrostei the pterygoquadrate and its associated bones are intimately associated with the cranium, and the functional jaw is composed of dermal bones, usually a pre-maxilla at the tip of the snout, followed by a maxilla on either side. Even in *Acipenser* (fig. 107) a membrane bone called a maxilla occurs on the pterygo-quadrate, but it is more like a dermopalatine. The quadrate part ossifies as a separate quad-rate bone which bears the artic-ular surface for the lower jaw.
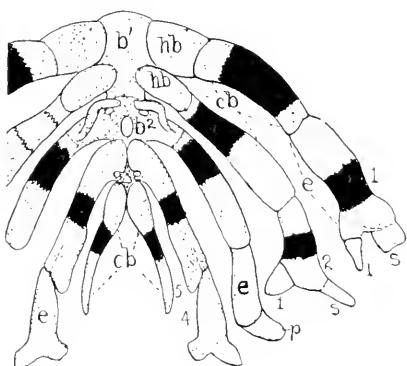
FIG. 102.—Branchial arches of *Acipenser sturio* (van Wijhe, '82). Bone, black; car-tilage stippled. *b*, basibranchial; *cb*, cerato-branchial; *e*, epibranchial; *hb*, hypobranchial. *i*, lower pharyngobranchial; *p*, pharyngo-branchial; *s*, suprapharyngobranchial.

The following bones may occur in connexion with the pterygoquadrate (fig. 74): At the extreme tip an **autopalatine** ossifying in the cartilage, and associated with a true (dermal) palatine, the compound bone usually articulating with the ectethmoid, occasion-ally extending farther forwards. The palatines are followed by two membrane bones, a more dorsal **entopterygoid** and a more ventral **ectopterygoid,** while farther back the cartilage ossifies above as **metapterygoid ;** below is the quadrate. Some of these five bones are sometimes absent; Siluroids, for example, having but palatine, meta-pterygoid and quadrate.

The posterior end of Meckel's cartilage ossifies as an articulare, said to fuse with a membrane bone, the goniale, which is probable, since in Tetrapoda the adult articulare often has such double origin.

Most of the rest of the Meckelian remains cartilage or is resorbed, but some Ganoids have a mentomeckelian developed on either side of the symphysis. The other bones of the lower jaw are dermal in origin, the most constant of these being a large dentale, usually toothed, and an angulare on the posterior and inferior parts of the jaw. Some Teleostomes have a splenial (two in *Amia*) on the medial side of the jaw, this occasionally bearing teeth. There is sometimes a strong coronoid process on the upper margin of the jaw for the insertion of the occludent muscles, and there may be a separate coronoid bone. Many fishes have a bone (**sesamoid articulare**) closely
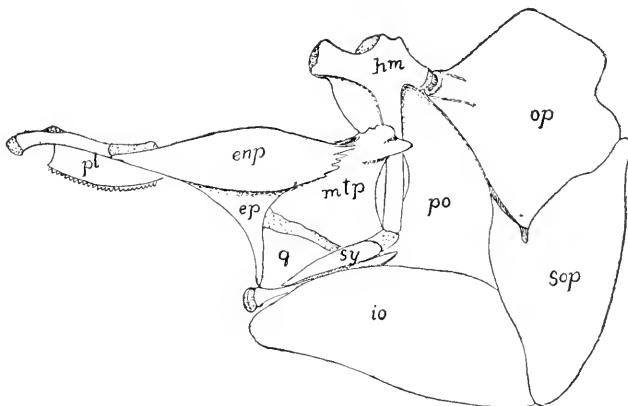
FIG. 103.—Pterygoids, suspensor and operculum of *Scomber* (Allis, '03). *enp*, entopterygoid; *ep*, ectopterygoid; *hm*, hyomandibula; *io*, interoperculum; *mtp*, metapterygoid; *op*, operculare; *pl*, palatine; *po*, preoperculum; *q*, quadrate; *sop*, suboperculum; *sy*, symplectic.

associated with the Meckelian, apparently an ossification of the tendon of the adductor mandibulæ muscle.

With ossification, the hyomandibular cartilage becomes two bones, an upper hyomandibula and a lower **symplectic** which connects with the quadrate. The hyale and branchial arches usually ossify directly without any membrane bones, but such sometimes occur. The extent of these ossifications varies greatly. The basihyal may extend in front of the hypohyals which it connects as a strong **os entoglossum (glossohyal)**, a part of which may come from a possible mandibular copula (p. 86). In several fishes the posterior side of the basihyal is connected with a vertical plate, the **thyreohyal**, which gives attachment for the retractor muscles of the hyoid apparatus. The rest of the copular structures varies considerably, that of the

7

branchial region being occasionally absent (*Lophius*), the arches ending freely below.

Another Teleostome characteristic is the presence of an opercular apparatus supported by membrane bones connected with the posterior side of the hyoid arch and covering the external openings of the gill-clefts. In its fullest development (figs. 74, 117) it consists of two parts, an upper **operculum** (gill cover) proper and a lower branchiostegal portion. The most constant of the bones of the upper part is an **operculare,** (really a lateral line bone, p. 74), articulated to a process of the hyomandibula (fig. 103). The operculare is usually overlaid in front by a **preoperculum** which also covers the outer side of hyomandibula and quadrate. Below and in part
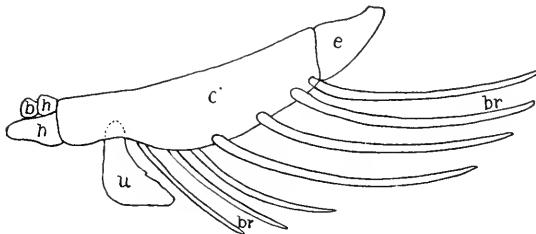
FIG. 104.—Hyale and branchiostegals of cod. *b*, basihyoid; *br*, branchiostegal rays; *c*, ceratohyoid; *e*, epihyoid; *h*, hypohyal; *u*, urohyal.

medial to the operculare is the **suboperculum,** and ventral to all of these and in the angle between them is the **interoperculum.** Only the operculare occurs in Chondrostei.

The branchiostegal part of the apparatus consists of a branchiostegal membrane supported by a series of usually slender membrane bones, the **branchiostegal rays,** attached largely or wholly to the ceratohyal. With these last are to be associated the **gular (jugular)** plates of many recent and fossil Ganoids and Elopidæ. In the extinct genera there may be a series of these along the inner margin of each half of the lower jaw, as far forwards as the symphysis. The number is reduced in modern Holostei, there being but a pair or (*Amia*) a single median plate.

GANOIDEA.—The skull of the lower Ganoids (Chondrostei) is very like that of Elasmobranchs, especially in the suspension of the jaws, ventral position of the mouth, the pterygoquadrate upper jaw, and the slight development of membrane bones. There are few cranial features which mark the group as a whole from the lower Teleosts, among them the presence of gular plates.

CHONDROSTEI.—Except in old individuals there are very few ossifications of the chondrocranium in Chondrostei, these being, probably, ectethmoids, orbito- and alisphenoids and prootics. The cranium passes behind into the vertebral column, the dorsal arches of which are fused. The roof is complete, with the exception of a small posterior fontanelle, and brain case and nasal capsules are not sharply separated, although the brain reaches forwards only to the orbital region. There is a long rostrum; the nares are far forwards, the nasal capsules being at the base of the rostrum. The barbels on the rostrum are supported by cartilage rods. Six vertebræ are fused to the hinder end of the cranium.

The numerous dermal bones of the roof of the adult skull are separated from the cartilage by perichondrium. A few of these (figs. 105, 106) are readily compared with those of other Vertebrates, among them dermoccipital, supracleithra, parietals, frontals, postorbitals,
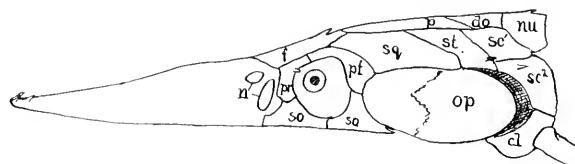
FIG. 105.

FIG. 106.

FIG. 105.—Side view of skull of *Scaphirhynchus*. *cl*, clavicle, and cleithrum; *do*, dermoccipital; *f*, frontal; *n*, naris; *nu*, nuchal; *op*, operculare; *p*, parietal; *pf*, post-frontal; *pr*, prefrontal; *sc*, supracleithra; *so*, suborbitals; *sq*, squamosal; *st*, supratemporal.

FIG. 106.—Skull of *Acipenser sturio*, the outline of the chondrocranium stippled (Gegenbaur, '98). *do*, dermoccipital; *fr*, frontal; *n*, nasal; *nu*, nuchal; *op*, operculare; *pa*, parietal; *pf*, prefrontal; *pof*, postfrontal; *sc*, supracleithrum; *sq*, squamosal; *st*, supratemporal.
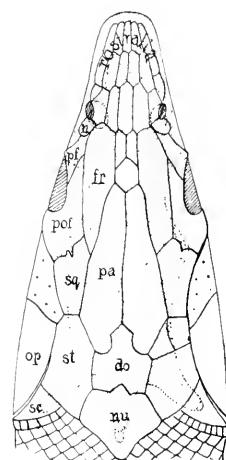
postfrontals and squamosals. The median series is continued backwards by an unpaired **nuchal bone** behind the dermoccipital. The ventral side of the cranium has a large parasphenoid extending from beneath the anterior vertebræ almost to the tip of the skull, a part of its anterior end being included in the cartilage cranial floor. It gives off a transverse process on either side which extends up under the postorbital region.

The jaws (fig. 107) are very primitive, consisting of pterygo-quadrate and Meckelian and are connected with the cranium by

only a hyomandibular suspensor, the pterygoquadrate being as truly the upper jaw as in any shark. Two or three bones occur in this jaw, one regarded as an entopterygoid (mesopterygoid) and a second doubtfully as a palatine, while some species have a metapterygoid of cartilage origin. The occludent border of the upper jaw is formed by a single maxilla on either side, which articulates with a second bone of doubtful homology, called both quadrate and preoperculum, but probably is neither. Meckel's cartilage is enveloped in a dentale, except behind where it articulates with the pterygoquadrate. The hyoid arch has passed beyond the Elasmobranch in the differentia-

FIG. 107.—Jaws of *Acipen-ser*. *pt*, pterygoid bone; *d*, dentale; *m*, maxilla; ?, bone called both quadrate and opperculare; cartilage stippled.

tion of a symplectic cartilage, articulating with both hyomandibula and the hinder end of the pterygoquadrate, the hyoman-dibula being connected with the postorbital process by ligament, and to the hyale by an interhyal cartilage. The rest of the visceral skeleton (fig. 102) calls for no remark, except that several of the elements are enveloped in ectochondrosteal bones, and the first and second gill-arches are connected with the cranium.

Polyodon has fewer bones than the sturgeons, the basis of the account above, and these are more difficult to homologise. Parietals, frontals, vomers and parasphenoid are evident; not so the others. The dorsal surface of the rostrum is covered with small ossicles, recalling similar bones on the snout of the garpike (infra). There is an anterior fontanelle and the only cartilage bones are those called pre- and opisthotic. The jaws have maxillæ and dentalia, with a mentomeckelian at the tip of the lower jaw. The ossifications of the other arches are like those of sturgeons, but are smaller.

Numerous extinct Ganoids allied to living Chondrostei have characters which make it probable that sturgeon and paddlefish of today are descendants of forms with crania more like those of normal Teleostomes. Details must be sought in paleontological textbooks.

CROSSOPTERYGII.—*Polypterus* and *Calamoichthys* of African rivers the only living Crossopterygians, are usually considered as relatives of a number of fossils ranging from Devonian to the cretace-ous, but these affinities have been questioned lately. For convenience living and fossil forms are considered together.

The chondrocranium of *Polypterus* only is known (figs. 108, 109, A). It is platybasic, the cranial cavity extending to the ethmoid region. The large

hypophysial fossa is perforate in the adult. The synotic tectum is considerable, and in front of it is a transverse bar with the epiphysial foramen, the bar separating anterior and posterior fontanelles. The thin-walled nasal capsules are connected by an internasal roof. A large fenestra between sphenolateral and trabecular cartilages gives exit to the optic nerve. There is a strong ridge on the otic capsule for articulation with the hyomandibula, and the posterior ends of the parachordals extend down around the aorta. The pterygoquadrate articulates in front with the ethmoid region, and its hinder end is supported by the hyomandibula which is dumb-bell-shaped, possibly indicating a symplectic part, though none occurs in the adult. The four gill-arches are very slender,
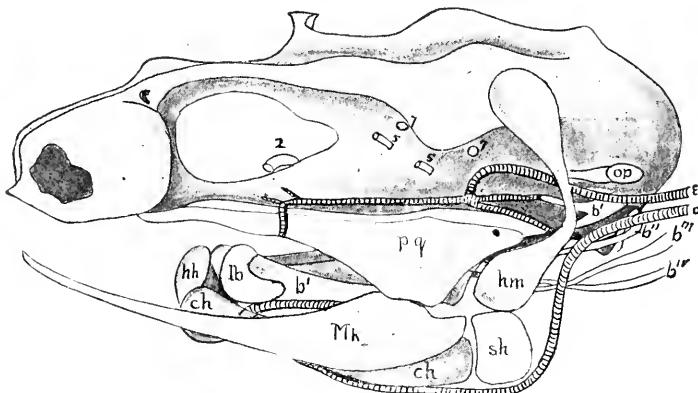
Fig. 108.—Chondrocranium of *Polypterus* (Budgett, '07). *b*, branchials; *ch*, ceratohyoid; *hh*, hypohyal; *hm*, hyomandibular; *lb*, labial; *mk*, Meckelian; *op*, operculum; *pq*, pterygoquadrate; *sh*, stylohyoid; 2–7, nerves.

the anterior reaching the cranium behind the hyomandibula. These arches are well ossified in the adult, some of them forming a suprapharyngeal bone as in many Teleosts.

The chondrocranium largely persists in the adult, but contains several cartilage bones (fig. 109, *A*) including mesethmoid, a pair each of ectethmoids, sphenotics and opisthotics. The hypophysial fossa is partly enclosed by bone, possibly representing ali- and orbitosphenoids, while the posterior part of the floor contains the fused basi- and exoccipitals, the latter meeting above the foramen magnum, no supraoccipital being ossified. The adult cranium (fig. 109, *B*) is covered by numerous membrane bones, some large, others small and apparently formed by fusion of a few scales. The cranial roof is formed by parietals, frontals and nasals, with a small **'adnasal'** in front of each nasal, and the mesethmoid visible between them. A

transverse row of supratemporals, supracleithra and dermoccipitals crosses the cranium behind. There is a lacrimal (prefrontal?) in front of the orbit; behind the opening is a postorbital or postfrontal, followed by a series of ossicles, one or more of them lateral to the spiracle. The margin of the upper jaw is formed by maxilla and premaxilla, the former followed by the preoperculum. The other opercular bones are an operculare and (except *Calamoichthys*) a suboperculum.

The roof of the mouth is lined by vomers and parasphenoid, both tooth-bearing, and a series (ecto-, ento-, and meta-) of pterygoids.

(A)   (B)
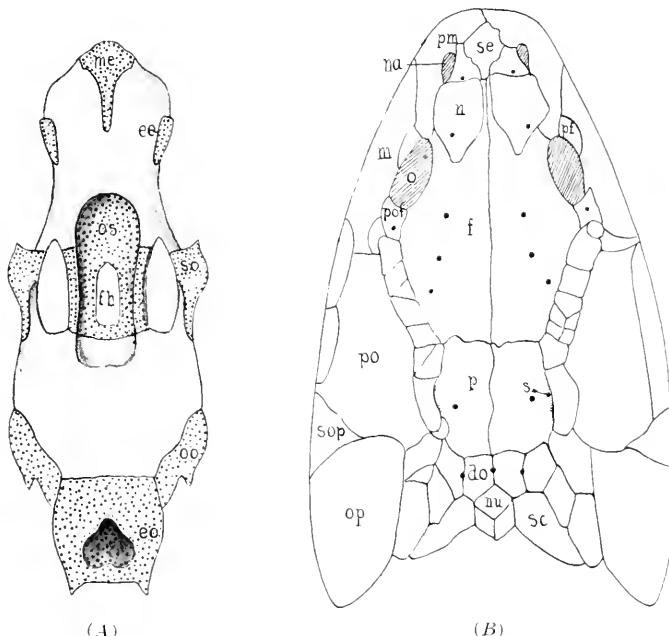
FIG. 109.—*A*. chondrocranium of nearly adult *Polypterus* with cartilage bones stippled (Butschli, '10); *B*, adult *Polypterus* (Wiedersheim, '86). *do*, dermoccipital; *ee*, ectethmoid; *eo*, exoccipital; *f*, frontal; *fh*, hypophysial fenestra; *m*, maxilla; *me*, mesethmoid; *n*, nasal; *na*, naris; *nu*, nuchal; *o*, orbit; *oo*, opisthotic; *op*, operculare; *os*, orbitosphenoid; *p*, parietal; *pf*, prefrontal; *pm*, premaxilla; *po*, preoperculum (?part postorbital); *pof*, postfrontal; *s*, opening of spiracle; *sc*, supracleithrum; *se*, supraethmoid; *so*, sphenotic; *sop*, suboperculum.

The bones of the lower jaw are dentale, splenial (with a coronoid process), and either angulare or goniale at the angle of the jaw. A labial cartilage (fig. 108) lies lateral to the jaw behind the coronoid process. A pair of gulars lie between the rami of the jaws; extinct

Crossopterygians (fig. 110) may have several gulars. The large
quadrate is loosely connected with the hyomandibula without a
symplectic.
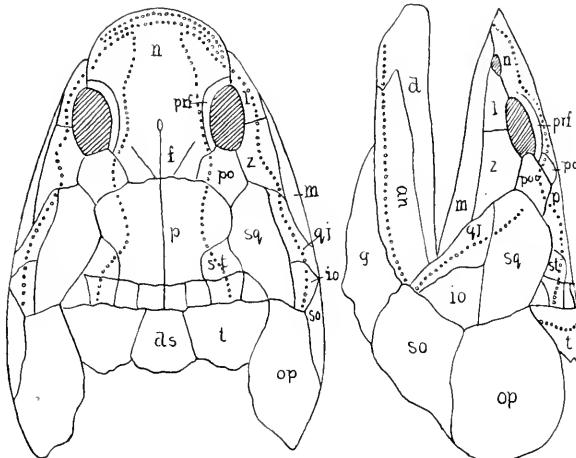
FIG. 110.—Skull of *Osteolepsis* (Gregory, '15, from Pander), lines of dots, lateral
line canals. *an*, angulare; *d*, dentale; *ds*, dermoccipital; *f*, frontal; *g*, gular; *io*, inter-
operculum; *l*, lacrimal; *m*, maxilla; *n*, nasal; *op*, operculare; *p*, parietal; *po*, postorbital;
prf, prefrontal; *qj*, quadratojugal; *so*, subopenculum; *sq*, squamosal; *st*, supratemporal;
t, tabulare; *z*, zygomatic.
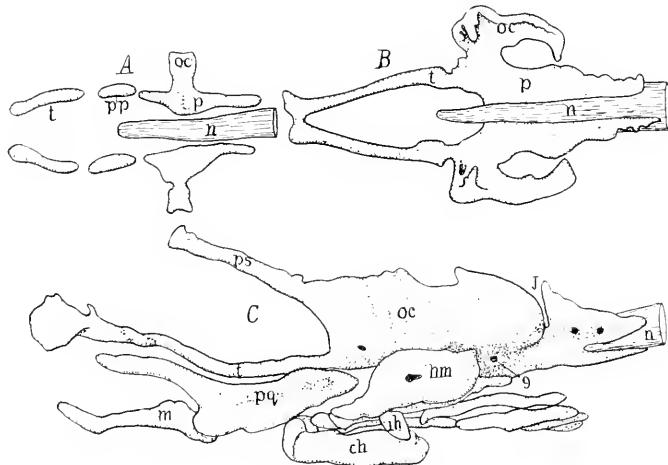
FIG. 111.—Chondrocrania of *Lepidosteus*. *A*, 10 mm. long; *B*, 11 mm.; *C*, 14 mm.
(Veit, '11). *ch*, ceratohyoid; *ih*, interhyal; *j*, jugular notch; *m*, Meckelian; *n*, notochord;
p, parachordal; *pp*, pole cartilage; *pq*, pterygoquadrate; *ps*, sphenolateral; *t*, trabecula.

HOLOSTEI.—The chondrocranium of *Lepidosteus* in the early stages
(fig. 111) has each trabecula in two parts (*A*) the posterior being the **polar
cartilage** of Veit. The sphenolateral joins the otic capsule (*C*) long before it is

connected with the trabecula. The early chondrocranium of *Amia* has several peculiarities. The trabeculæ are widely separated from the anterior end of the notochord, but meet it further back; they unite in front as a narrow mesethmoid and then diverge as cornua which are joined by the anterior ends of the pterygoquadrates. The large otic capsules are widely open to the brain cavity. The hyomandibula, perforated for the hyomandibular nerve, is fused with the otic capsule and its lower end is a narrow symplectic process extending towards the angle of the jaw. The sphenolateral cartilage, appearing later, is separated from the trabecula by a wide gap, both cartilages meeting in the nasal capsule which has a fenestrated roof, the capsules of the two sides being separated by a wider ethmoid plate. The cartilage roof of the cranium is added later and is complete, without fontanelles. Three vertebral arches are absorbed in the occipital region.

Several bones develop in the chondrocranium, none needing detailed description, and little more need be said of the membrane bones of *Amia*, save that the one here called supraethmoid is often called ethmoid, but is membrane in origin.   The so-called intercalare
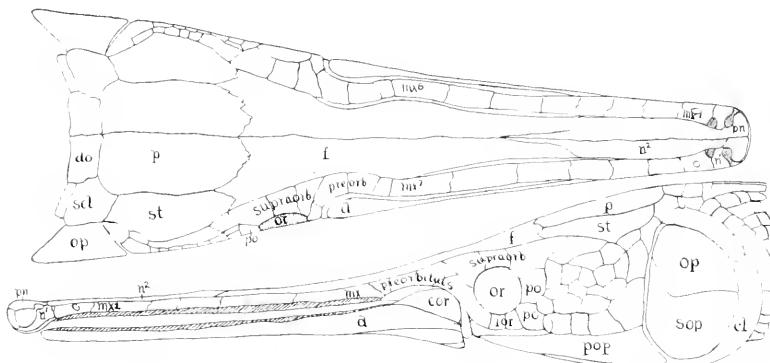
FIG. 112.—Skull of *Lepidosteus*. *cl*, clavicle; *cor*, coronoid; *d*, dentale; *do*, dermoccipital; *f*, frontal; *ior*, infraorbitals; *mx*, maxillary ossicles; *n*, nasal; *op*, operculare; *or*, orbit; *p*, parietal; *pn*, prenasal; *po*, postorbital; *pop*, preoperculum; *scl*, supracleithrum (posttemporal); *sop*, suboperculum; *st*, supratemporal.

is probably opisthotic. The other bones are much like those of lower Teleosts, the absence of a supraoccipital separating *Amia* from most bony fishes.

Lepidosteus differs in several respects from other Teleostomes. Nasal and premaxilla are apparently fused in the tip of the snout, and in front of them is a **prenasal** on either side. Instead of a single premaxilla there is a series of maxillary ossicles, each bearing teeth. The orbit is surrounded by orbital bones, the preorbitals extending some distance in front of the orbit. The squamosal is

replaced by a number of 'cheek bones.' Parasphenoid and vomer are long and slender, and the pterygoquadrate series has the quadrate shifted to the anterior end of the entopterygoid, bringing the hinge of the jaw some distance in front of the orbit. The hyomandibula is movably attached to the otic capsule; it articulates below with a slender symplectic which has no connexion with the quadrate except by way of the interoperculum. The five branchial arches are well developed except the last which consists of a single element, apparently the fused cerato- and hypobranchial. The broad basihyal, covered dorsally by bone, extends into the tongue as an os entoglossum. The pharyngobranchials of arches 2 to 4 are divided into superior and inferior elements, and all of the arches are connected with the posterior part of the cranium.

TELEOSTEI.—This great group, with its thousands of species, shows a great variety in form of skull, but the differences are largely those of form, less of presence or absence or different relations of the separate bones. The lower groups are much like the Holostei, the line between them being negligible so far as skull is concerned. From the lower Teleosts there is a gradual progress through the whole series to the most specialized forms. Hence it is impossible, without greatly exceeding the limits of the present work, to begin to enumerate all of the conditions which occur. In fact, the lower members of the group are better known than the higher and more aberrant forms, and there has been no general survey of our knowledge for years. No group of Vertebrates needs a comparative study more than do the Teleosts.

The development of the skull has been studied in few species and those mostly Physostomes (p. 92) where the structure is much like that of *Amia*. In these the cranium is platybasic (fig. 96), the cranial cavity extending to the ethmoid region. The higher species have a tropibasic cranium (fig. 97), the great development of the orbits so constricting the skull in the interorbital region that the brain cannot extend beyond the alisphenoid bones.

The otic capsules sometimes arise in continuity with the parachordal plates, sometimes independently. Several vertebræ (*Carassius* 3, *Salmo* 5) are absorbed in the occipital region. The trabeculæ at first are in a plane with the basal plate, and in front they unite in a broad ethmoid plate which extends laterally beneath the nasal organs. In platybasic crania the trabeculæ are distinct as far forwards as the ethmoid plate; in tropibasic they unite to a trabecula communis a little in front of the hypophysis.

There may be several fenestræ in the chondrocranial floor, among them a basicapsular between the parachordal and otic capsule, the ninth nerve in some

genera passing through it, behind it in others.   Basicranial fenestræ, anterior
and posterior, may occur nearer the median line, the anterior often being
confluent with the hypophysial fenestra, the posterior partly or wholly divided
into right and left halves by the notochord.   The walls of the posterior part of
the chondrocranium are formed by the occipital vertebræ and the otic capsules,
the latter widely open on the medial sides.   In the interorbital region of platy-
basic crania there is no constriction, the walls being formed by trabeculæ and
sphenolaterals.   In tropibasic skulls an interorbital septum extends upwards
from the common trabecula, this when high, restricts the brain to the postorbital
parts.   In all species a narrow **marginal band** (sphenolateral) of cartilage
extends, dorsal to the orbit, from otic
capsule to the roof (tegmen) of the
anterior part of the skull.   This
anterior tegmen is wide in some fishes,
narrow in others where it lies in or
behind the plane of the pineal organ.
There is always a posterior fontanelle,
an anterior also when the anterior
tegmen is narrow.   The posterior
fontanelle is limited behind by the
synotic tectum and is often divided
into right and left halves by a nar-
row cartilage bar extending from the
tegmen towards or to the synotic
tectum, a remnant of the complete
Elasmobranch roof.

FIG. 113.—Three successive stages in the
development of the chondrocranium of
Salmo fario (Woskoboynikow in Schimp-
kewitsch, '21).   First stage black; second
stippled; third shaded.   *ct*, trabecular cornu;
e, ethmoid plate; *h*, hypophysis; *n*, noto-
chord; *oc*, otic capsule; *pc*, parachordal; *ps*,
sphenolateral; *st*, synotic tectum; *t*, tra-
becula; *tc*, tegmen cranii.

The nasal organs are separated
by a median nasal septum, a con-
tinuation of that in the interorbital
region.   The floor of each capsule is
formed by the lateral part of the eth-
moid plate, the roof is an expansion
of the tegmen.   Behind, the capsule
is limited by a cartilage, the homo-
logue of the antorbital crest of sharks.
In Siluroids, Cyprinoids and Gadids
the olfactory nerve follows the normal course inside the cranial cavity from
brain to olfactory organ.   In many other Teleosts, as a result of the interorbital
septum, the nerve enters the orbit and then reaches the nasal cavity by passing
through the antorbital crest.

The visceral skeleton arises much as in Elasmobranchs, except that it is
largely ossified in the adult.   The pterygoquadrate has its pterygoid part
joining the ethmoid by one or two processes, and associated with it may be a few
isolated cartilages (a **subrostral** in *Salmo*, **submaxillary** in *Catostomus* and
Perca, and one at the angle of the mouth in many genera).   These are regarded
as remnants of labial cartilages (p. 68).   The quadrate part of the pterygo-

quadrate appears first, the pterygoid process growing forwards from this, the quadrate part always remaining the larger. Meckel's cartilage offers nothing of importance. In the precartilage stage the hyoid arch consists of three elements on a side (hyomandibula, symplectic and the upper part of the hyale), the hyomandibula forming around the hyomandibular nerve, the foramen often persisting in the adult. The gill-arches appear in order from in front backwards, the last being the most rudimentary, the fourth frequently lacking the hyobranchial, the fifth being even more reduced. At first hyoid and gill arches are connected by a continuous copula which segments later into an anterior basihyal, prolonged forwards as an (often separate) entoglossal, followed by a varying number of basibranchials.
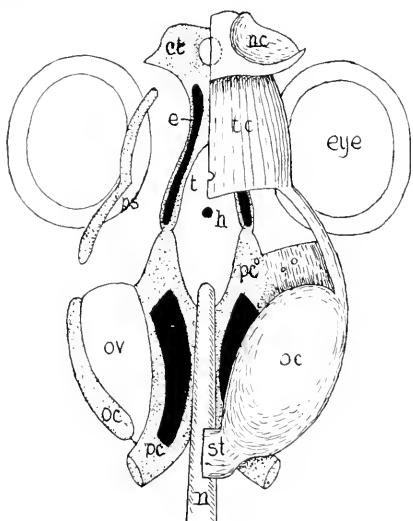
A peculiarity of many adult Physostomes (Siluroids excepted) and Acanthopterygians, is an **eye-muscle canal (myodome)** which contains two of the rectus muscles of the eye. It is formed early (before much ossification) and seems to have arisen as a result of reduction of the medial wall of the orbit, forcing the muscles to obtain another origin. The muscles grow back between brain and basal plate, sometimes extending so far as to pass out of the cranial cavity behind, their ends lying ventral to the basal plate and between it and the developing parasphenoid. In typical conditions processes from the two prootics meet in the middle line, roofing the anterior part of the canal, the posterior being excavated in the basioccipital and floored by the parasphenoid. The tube may be divided, an upper part containing the hinder part of the external rectus, the lower that of the internal rectus muscle. Usually the canal extends to the occipital region and may be open behind or end blindly.

Some of the most interesting modifications of the skull occur in Pleuronectids. At first these fishes are bilaterally symmetrical and swim in the normal position. Then the young turn on one side, lying hereafter with that side downwards. This change of position results in the transfer of the eye from the lower to the upper side, twisting the bones and destroying the primitive symmetry of the anterior part of the cranium, the posterior part remaining nearly normal (fig. 114).

The four occipitalia usually ossify in the base of the cranium. The supraoccipital has a marked dorsal crest, often produced backwards as an occipital spine to which the dorsal trunk muscles are attached. This bone usually separates the parietals when these are present, and extends forwards to the frontal, but sometimes the parietals overlap the supraoccipital, occasionally meeting in the

median line.   The supraoccipital is sometimes excluded from the
border of the foramen magnum by the exoccipitals.   The exoccipitals,
pierced by the ninth and tenth nerves (sometimes by the spinooccip-
itals), usually meet below the foramen, excluding the basioccipital
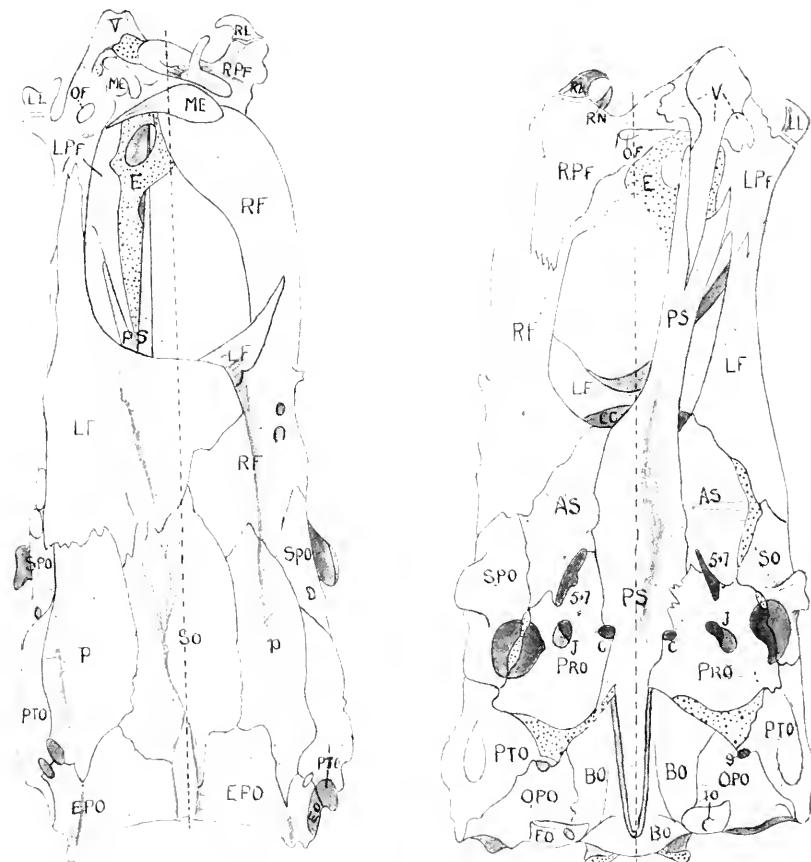
Fig. 114.—Dorsal and ventral sides of skull of *Pleuronectes* (Cole and Johnstone,
'01); dotted lines show planes of symmetry. *as*, alisphenoid; *bo*, basioccipital; *c*,
carotid foramen; *cc*, cranial cavity; *e*, ethmoid cartilage; *eo*, exoccipital; *epo*, epiotic;
j, jugular foramen; *lf*, left frontal; *lpf*, left prefrontal; *of*, olfactory foramen; *opo*, opis-
thotic; *p*, parietal; *pro*, prootic; *ps*, parasphenoid; *pto*, pterotic; *rf*, right frontal; *rl*,
right lacrimal; *rn*, right nasal; *rpf*, right prefrontal; *so*, supraoccipital; *spo*, sphenotic;
v, vomer; 5–10 nerve exits.

from its wall.   In Ostariophysiæ an internal process from each
exoccipital forms the floor of the posterior part of the brain cavity, the
space below being occupied by the vestibular sacs of the ear, while
in Cyprinoids (fig. 115) a foramen in each exoccipital connects the

Weberian apparatus (a series of ossicles developed from the vertebræ and connected with the air-bladder) with the ear. In some of the higher Teleosts the exoccipital has a process for articulation with the first vertebra. The basioccipital is usually opisthocœle, bears no condyle, the cavity being occupied by remains of the notochord. In several Symbranchs it receives the conical centrum of the first vertebra, and in *Fistularia* the bone has a true condyle.

The sphenoid cartilage rarely ossifies in the middle line, there being a parasphenoid ventral to the cartilage and, at least in some genera, a **suprasphenoid** (membrane bone) inside the cranial wall and dorsal to it. The alisphenoids (**alæ temporales**) lie between the orbit and the exit of the fifth and seventh nerves. They may be widely separated below by parasphenoid and suprasphenoid, or may meet dorsal to the latter. They may share in the cranial wall, or a process from the frontal may meet one from the parasphenoid, excluding the alisphenoid from the wall. They are reduced in tropibasic skulls, and in some cases (*e.g.*, *Cyprinus*) they afford attachment to a part of the hyomandibula. Orbitosphenoids are absent from tropibasic skulls, the Berycoids, *Regalecus*, *Lampris* and *Velifer* excepted. In platybasic crania they arise as paired bones which often fuse in the middle line, the orbital foramen lying between them and the ectethmoids.

FIG. 115.—Base of cranium of Carp (Zittel, '87). *a*, for dorsal aorta; *bo*, basioccipital; *eo*, exoccipital; *ep*, epiotic; *f*, foramen magnum; *so*, supraoccipital; *x*, foramen for connexion of Weberian apparatus with ear.

A large part of the mesethmoid region persists as cartilage, but its dorsal surface is covered by a dermal **supraethmoid** which sometimes persists as a distinct bone, but usually fuses with the underlying mesethmoid ossification. The ectethmoid of either side, which lies in front of the orbit, ossifies as an ectethmoid bone, always covered by a prefrontal of dermal origin, the compound bone being called by either name (also **pleurethmoid**). It forms the anterior wall of the orbit and in most Teleosts the nasal cavity extends into it, the olfactory nerve either perforating it or running between it and the mesethmoid.

The otic capsule has more bones developed in and on its wall than occur in other classes of Vertebrates, some being compound bones, the parts so intimately associated that the lens or even ontogeny is

necessary to distinguish them. Prootic and epiotic are constant. The prootic (petrosal) the largest of these, forms the floor and most of the lateral wall of the labyrinth, the bones of the two sides usually fusing in the middle line behind the hypophysis and dorsal to the parasphenoid. The epiotic (**occipitale externum** of older works) forms the postero-lateral angle of the cranium, extends to the base of the skull and bounds the posterior semicircular canal, besides affording attachment for the supracleithrum. The opisthotic, more ventral in its position, is often absent; when present it is frequently excluded from the labyrinthine wall. The sphenotic is often, next to the frontal, the most conspicuous bone of the dorsal surface, and, although a cartilage bone, is often called postfrontal. Its lateral surface in most fishes is grooved for a part of the hyomandibula, and it is overlaid by a dermal bone, possibly the true postfrontal. The pterotic ossifies in the capsular wall above the lateral semicircular canal and is covered externally by the squamosal, the two frequently fusing to a **squamoso-pterotic bone,** the squamosal part being traversed by a lateral line canal. When the sphenotic is small, the squamosal may articulate with the frontal, from which it is usually separated by the parietal.

In connexion with the otic capsule it may be noted that frequently the inner ear contains, instead of the minute otoliths of most Vertebrates, one or more large calcifications ('ear-stones'), irregular in shape and particularly large in Sciænoids.

When fullest developed the pterygoquadrate arch (fig. 103) is a series of bones, some dermal, some cartilage in origin. The series has been outlined above, (p. 71), and the following statements are additional. The ectopterygoid (epipterygoid) is on the ventral side of the pterygoid process and below the ento- (meso-) pterygoid. The ectopterygoid usually extends along the anterior border of the quadrate, but sometimes a part of the entopterygoid intervenes. There is an intimate relation between pterygoquadrate and hyoid arches, both metapterygoid and quadrate being closely associated with the hyomandibula, the first directly, the other usually by the intervention of the symplectic, although a direct connexion may occur. The articulare is the only cartilage bone known in the lower jaw. It is usually coossified with the goniale, the distinction between the two being recognizable only in development, but they may remain separate in many Clupeids.

Membrane bones are greatly reduced, or even completely absent from Plectognaths and Pediculati. In other fishes the frontal (paired in development, fusing early) is the largest membrane bone on the dorsal surface. In Physostomes it extends from supraoccipitals to nasals, or, when these are separate, to the supraethmoid. In most Physoclists the parietals come between supraoccipital and frontal, and rarely (*Mormyris*) an interparietal also occurs. Frequently anterior and posterior ends of the frontal are incised by narrow fontanelles, and in a few forms the frontal is excluded from the wall of the cranial cavity. Its participation in the anterior wall of the cavity was noted above (p. 109). The Siluroids excepted,
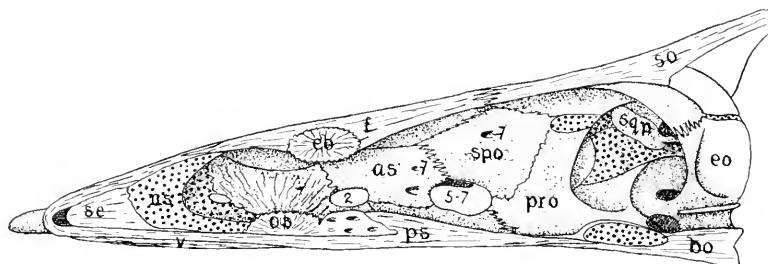
Fig. 116.—Interior of cranium of *Amiurus* (Kindred, '19). *as*, alisphenoid; *bo*, basioccipital; *eb*, epiphysial bar; *eo*, exoccipital; *f*, frontal; *ns*, nasal septum; *os*, orbitosphenoid; *pro*, prootic; *ps*, parasphenoid; *se*, supraethmoid; *so*, supraoccipital; *spo*, sphenotic; *sqp*, squamoso-pterotic; *v*, vomer.

the parietals are paired, though reduced in Synentognaths. Pre- and postfrontals, supraethmoid and squamosals are noticed with the cartilage bones.

The circumorbital bones (fig. 100) arise as protection to the lateral line canals and in the more primitive Teleosts are tubular. Of them the supraorbitals are least constant, and when present, are small. There are usually four infraorbitals. Some of these are enlarged in Loricati into plates which give the name 'mail-cheek' fishes to this group. The last infraorbital has a 'stay,' a strong process extending back as a support for the spine of the preoperculum.

The bones (premaxilla and maxilla) of the upper jaw afford characters utilized in systematic ichthyology. Usually the maxilla is the longer and in a few cases, (recalling *Lepidosteus*) is divided into two or more ossicles. On the other hand it is lacking in a few species (some Siluroids, *Anguilla*, etc.). In Acanthopterygii, Anacanthini, some Pharyngobranchs, Cyprinoids, etc. the maxilla is medial to and

parallel with the premaxilla, the latter alone forming the functional margin of the jaw, and, except in some Acanthini, alone bearing teeth (lacking on the premaxilla of some eels). In these forms the upper jaw, and especially the premaxilla, rests on a cartilage (probable homologue of the first upper labial) and has great mobility, the premaxilla often having an ascending process connected with the cranium by an elastic ligament. In some Teleosts the mobility is largely or wholly lost, the premaxilla being firmly attached to the ventral side of the supraethmoid. The premaxilla is greatly elongate
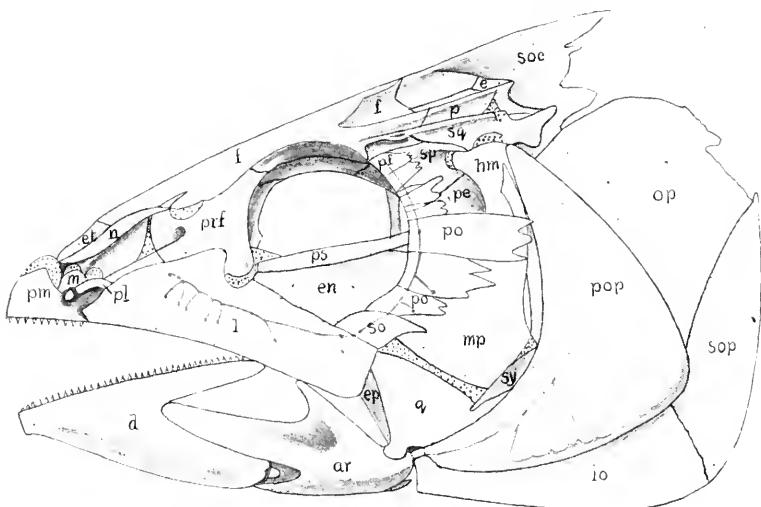
FIG. 117.—Skull of *Scomber* (Allis, '03). *ar*, articular; *d*, dentale; *en*, entopterygoid; *e*, exoccipital; *ep*, ectopterygoid; *et*, ethmoid; *f*, frontal; *hm*, hyomandibula; *io*, inter-operculum; *l*, lacrimal; *m*, maxilla; *mp*, metapterygoid; *n*, nasal; *op*, operculare; *p*, parietal; *pe*, petrosal; *pf*, postfrontal; *pl*, palatine; *pm*, premaxilla; *pop*, preoperculum; *po*, postorbitals; *prf*, prefrontal; *ps*, parasphenoid; *soc*, supraoccipital; *so*, suborbital; *sop*, suboperculum; *sp*, sphenotic; *sq*, squamosal; *sy*, symplectic.

in a few fishes (*Belone, Xiphias*) and, with the vomer and maxilla, forms the sword of swordfish. Maxilla and premaxilla are fused in Gymnodonts, and in *Diodon* and *Mormyrus* the premaxillæ of the two sides are united.

The membrane bones of the oral roof are much as outlined on p. 94; the pterygoids were noticed above. The thin and elongate parasphenoid extends from the basioccipital which it overlaps, to the vomer. Its relations to the eye-muscle canal were mentioned above. The vomer of the adult is broader in front and tapers backwards. In *Amiurus* it arises from a single centre, from a pair in

Esox. It often extends dorsally to the bones of the roof. It usually is toothed, the teeth arising independently of the bone.

The bones of the lower jaw may include, in ontogeny, articulare, goniale, angulare, coronoid, sesamoid articular and dentale, with
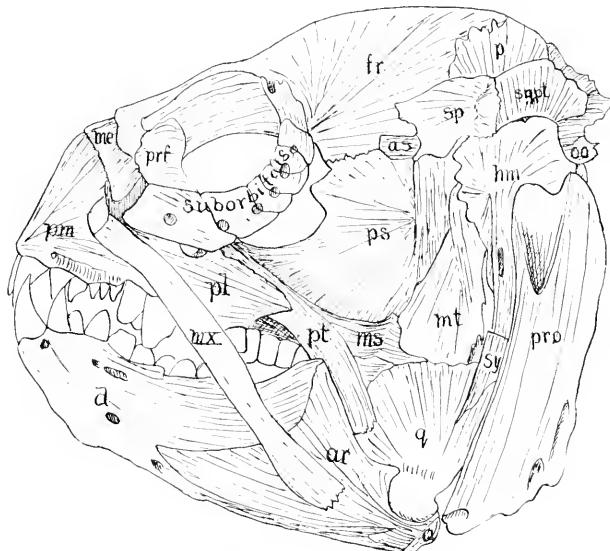
FIG. 118.—Skull of *Anarrichthys* (Adams, '09). *a*, angulare; *ar*, articulare; *as*, alisphenoid; *d*, dentale; *fr*, frontal; *hm*, hyomandibula; *me*, mesethmoid; *ms*, entoptery-goid; *mt*, metapterygoid; *mx*, maxilla; *oo*, opisthotic; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *prf*, prefrontal or lacrimal; *pro*, preoperculum; *ps*, parasphenoid; *pt*, ecto-pterygoid; *q*, quadrate; *sp*, sphenotic; *sqpt*, squamoso-pterotic; *sy*, symplectic.
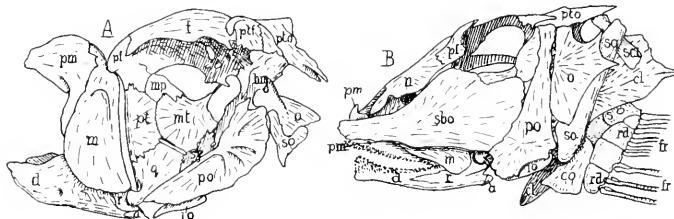
FIG. 119.—Skulls of (*A*) *Dicotylichthys punctulatus* and (*B*) *Trigla gurnardus* (Goodrich, '09). *a*, angulare; *cl*, cleithrum; *co*, coracoid; *d*, dentale; *f*, frontal; *hm*, hyomandibula; *io*, interoperculum; *m*, maxilla; *mp*, mesopterygoid; *mt*, metapterygoid; *n*, nasal; *o*, operculare; *pf*, prefrontal; *pm*, premaxilla; *po*, preoperculum; *pt*, pterygoid; *ptf*, postfrontal; *pto*, pterotic; *q*, quadrate; *r*, articulare; *rd*, radialia of fin; *s*, scapula; *sbo*, subocular, enlarged; *so*, suboperculum; *sy*, symplectic.

rarely a splenial. These mostly fuse, the extreme of this being in Plectognaths where there are but two bones in either half of the jaw.

Part of the dentale is described as arising from cartilage (possibly a mentomeckelian) and it frequently has a vacuity on the medial side.

As in Ganoids, the hyoid arch consists of the suspensor and the hyale, the latter extending into the floor of the mouth. At most, the suspensor consists of hyomandibula and symplectic (the latter absent in some Physostomes). The hyomandibula is firmly fixed to the cranium (not ankylosed) in Plectognaths; elsewhere it is movable. Sometimes it has a single head which articulates with the opisthotic; others have also an anterior head which connects with the sphenotic or even as far forwards as the alisphenoid. It articulates in front with the metapterygoid; below either with the quadrate directly or by a symplectic which varies in size.

A small interhyal (**stylohyal**) connects hyomandibula and hyale. The hyale is divided into epi-, cerato- and hypohyal, the latter element of the two sides being connected by a basihyal which sometimes extends as an entoglossum into the tongue, this sometimes covered by a **dermentoglossum,** arising by the fusion of dentinal bases. The opercular apparatus is connected with the hyoid arch, its parts and relations suggesting homology with the hyoid radials of Elasmobranchs, a comparison negatived by the dermal origin of the opercular bones. The operculum, when fully developed, has the parts enumerated above (p. 98). The operculare is hinged to a process on the posterior side of the hyomandibula, the suboperculum being connected by membrane to operculare and interoperculum. The branchiostegal bones are usually slender, sometimes one or more are expanded to broad plates. Some Elopids have gular plates. The branchial arches, usually five, are reduced at the hinder end of the series. Typically each is divided as in sharks, (p. 65), the halves of each arch being connected ventrally by a basibranchial. The pharyngobranchials (**suprabranchials**) usually lie longitudinally and side by side, beneath the cranium and not infrequently all are fused to a single **suprapharyngeal bone.** Usually they bear teeth and in Cyprinoids they receive support from a projection from the floor of the skull. These suprapharyngeals act in opposition to the cerato- and hypobranchials (**inferior pharyngeals**), both serving as pharyngeal jaws, the resemblance to true jaws being greatest in the Pharyngognaths where the lower bones of the two sides unite to a single plate. The teeth on these pharyngeals are supported on plates of membrane bone (superior and inferior **dermopharyngeals**),

connected respectively with pharyngo- and epibranchials. Usually all of the arches bear wart-like or longer projections ('gill-rakers' or 'strainers') on their anterior and posterior sides, these serving to strain small particles taken in with the water through the mouth.

DIPNOI.—The development of the cranium (figs. 120, 121) is known only in *Ceratodus*, where in the earliest stage described the parachordals extend as far as the tip of the notochord but do not reach the otic capsules. The orbital walls are formed by trabeculæ and sphenolateral cartilages, neither extending forwards beyond the optic nerve. The otic capsules are still procartilage and the rod-like pterygoquadrate touches the cranium with its anterior end at the junction of basal plate and trabecula. In a much later stage the chondrocranium is a connected whole, except that the three occipital vertebræ are continuous with only the epichordal cartilage. Sphenolaterals have now united with the otic capsules above the fifth and seventh nerves, the trabeculæ below with the basal plate. There is no trace as yet of a cranial roof and the ninth nerve passes through the otic capsule. The interorbital wall is continuous, the trabeculæ extending to the tip of the snout. Near the

FIG. 120.—Early chondrocranium of *Ceratodus* (Sewertzoff, '02). *e*, eye; *oc*, procartilage of otic capsule; *ov*, otic vesicle; *p*, parachordal; *q*, quadrate; *s*, spiracle; *sl*, sphenolateral; *t*, trabecula; *2*, optic nerve.

orbit is a process (posterior labial of Huxley, Sewertzoff's **ethmoidal process**) directed outwardly and downwards, which persists in the adult. The trabeculæ pass medial to the olfactory organs and fuse in front. Two processes given off
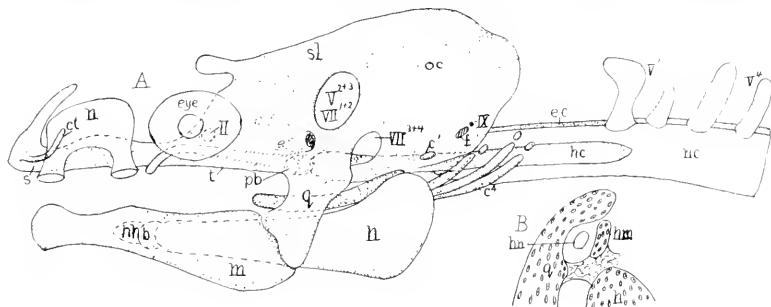
FIG. 121.—Late chondrocranium of *Ceratodus*; *B*, hyoid and hyomandibula in later stage (Sewertzoff, '02). *b*, basihyal; *c*, ceratobranchial; *ct*, trabecular cornu; *ec*, epichordal cartilage; *h*, hyoid; *hc*, hypochordal cartilage; *hh*, hypohyal; *hm*, hyomandibula; *hn*, hyomandibular nerve; *m*, Meckelian; *n*, nasal capsule; *nc*, notochord; *oc*, otic capsule; *pb*, palatobasal process; *q*, quadrate; *s*, nasal septum; *sl*, sphenolateral region; *t*, trabecula; *v*, vertebræ; II–IX, nerve exits.

from this region on either side, the lower comparable to the cornua, the upper forming the roof of the nasal capsule. The cranium is platybasic, the hypophysial fenestra large.

The pterygoquadrate is now firmly united with the cranium by three proc-
esses—otic to the capsule, palatobasal to the trabecula and ascending (epiptery-
goid) to the sphenolateral region, conditions strikingly like those in Urodeles.
The ventral end of the quadrate region articulates with the Meckelian, and a
process on the hinder side of the quadrate connects with the hyoid arch, a small
cartilage (interpreted by Sewertzoff as hyomandibula, fig. 122, B) being con-
nected with both otic process and otic capsule (Huxley found a hyomandibula,
Pollard's opercular cartilage, in the same position in the adult). There were
four branchial arches in this stage, the fifth appearing a little later, each with a
small epibranchial and a larger ceratobranchial. There is no copula, but the
adult has a long one connecting the basihyal with the first ceratobranchial.
There is none in other Dipnoan genera.

The cartilage skull is little ossified in the adult, scarcely more than
in Chondrostei. There is a pair of exoccipitals, and in the visceral
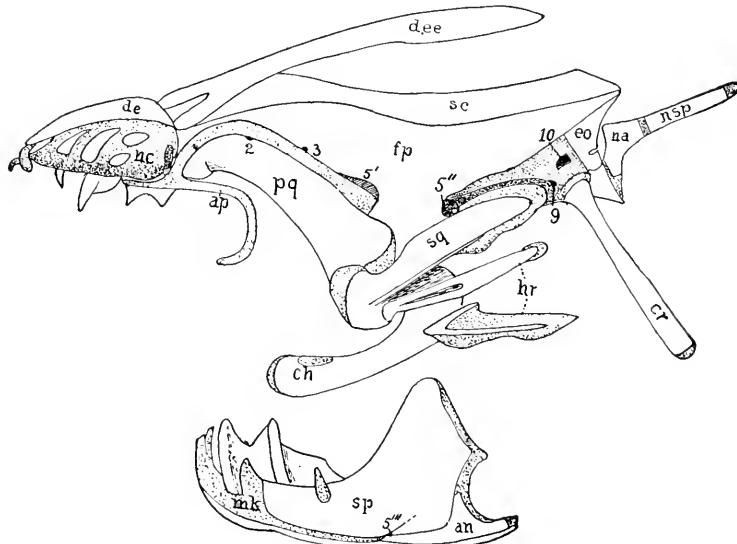
FIG. 122.--Skull of *Lepidosiren* (Bridge). *an*, angulare; *ap*, antorbital process;
ch, ceratohyal; *cr*, cranial rib; *de*, dermal ethmoid (?supraethmoid); *dee*, dermal ecteth-
moid; *eo*, exoccipital; *fp*, fronto-parietal; *hr*, 'hyoidean rib;' *mk*, Meckel's cartilage;
na, first neural arch; *nc*, nasal capsule; *nsp*, neural spine; *pq*, pterygoquadrate; *sc*,
sagittal crest of fronto-parietal; *sp*, splenial; *sq*, squamosal 2–10, nerve exits.

arches only the ceratohyals ossify. The membrane bones are more
numerous, but far fewer than in most fossil relatives or in other fishes,
and there is no little difficulty in tracing homologies of many of those
present. Overlying the middle of the ethmoid region is a median
bone called both dermethmoid and nasal. This is followed by a
second unpaired bone, long and slender in *Protopterus*, wider in

Lepidosiren and widest in *Ceratodus*, usually regarded as a fronto-
parietal; it usually extends almost to the posterior end of the cranium.
In *Ceratodus* this frontoparietal is bounded on either side by a bone
called both supraorbital and dermal ectethmoid, which extends from
the nasal nearly to (*Ceratodus*) or beyond the hinder end of the skull
(*Lepidosiren*). In the latter genus these supraorbitals overlap the
sides of the frontoparietals; in *Protopterus* they meet in front, dorsal
to that bone. *Ceratodus* has a 'squamosal' articulated by its whole
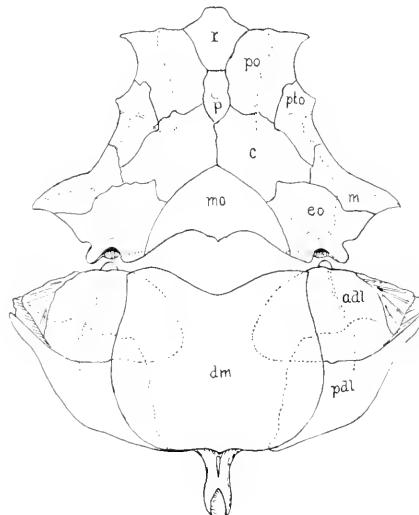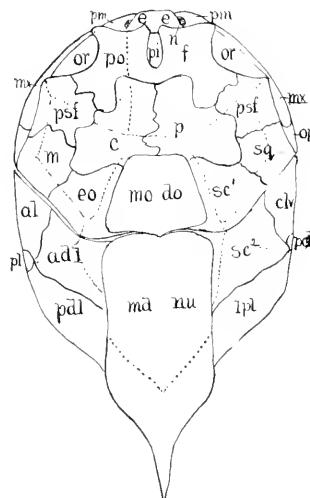
FIG. 123.   FIG. 124.

FIG. 123.—Dorsal armor of *Dinichthys intermedius* (Hussakoff, '05). Dotted lines,
lateral line canals; cranium and trunk armor separated. *adl*, anterior dorsolateral; *c*,
central; *dm*, dorso-median; *eo*, external occipital; *m*, marginal; *mo*, median occipital;
p, pineal; *pdl*, posterior dorsolateral; *po*, *pto*, pre- and postorbital; *r*, rostral.

FIG. 124.—Dorsal side of head of *Coccosteus* (Traquair from Woodward '98).
Left gives the usual interpretation of parts, right that of Bütschli; dotted lines position
of lateral line organs. *adl*, anterior dorsolateral; *al*, anterior lateral; *c*, central; *clv*,
clavicle; *do*, dermoccipital; *e*, ethmoid; *eo*, exoccipital; *f*, frontal; *lpl*, lateral plate; *m*,
marginal; *md*, median; *mx*, maxilla; *n*, naris; *nu*, nuchal; *op*, operculum; *or*, orbit;
p, parietal; *pcl*, postclavicle; *pdl*, posterior dorsolateral; *pi*, pineal; *pl*, posterior lateral;
pm, premaxilla; *po*, preorbital; *psf*, postfrontal; *sc*, supraclavicle; *sq*, squamosal.

length to the supraorbital, in *Lepidosiren* by a narrow process; in
Protopterus it is separated by a considerable interval, and in all three
it extends ventrally over the outer surface of the quadrate. *Cerato-
dus* has a postorbital in front of the squamosal, the first of a series of
lateral line bones, extending forwards (suborbitals) beneath the eye.
These do not occur in the other genera.

Fusion of the quadrate to the cranium produces autostyly. A bone (apparently dermal) extends from the quadrate forwards in the roof of the mouth and is called 'palato-pterygoid,' the bones of the two sides meeting in front and supporting a large tooth-plate on either side, while farther forwards *Ceratodus* has a pair of 'vomerine' teeth. A large parasphenoid extends from palatopterygoid to about the hinder end of the skull. Meckel's cartilage persists in the lower jaw and is bounded on the medial side by a large tooth-bearing plate. Below is an angulare; no articulare is ossified. The rest of the visceral skeleton is largely degenerate, the hyoid arch being best preserved. In *Ceratodus* it has several parts; in the others it is a single bone bearing a so-called interoperculum on its posterior surface.

A number of fossils are more or less closely related to the existing Dipnoi, some differing but little from them, but others, frequently grouped as ARTHRODIRA, are very dissimilar. This name alludes to the fact that the skull, composed of a limited number of bones, is movably articulated with the armor plates of the trunk, which may occur on both dorsal and ventral sides. Some genera, like *Coccosteus* (fig. 124) have crania in which some homologies can be traced with other Vertebrates, but other plates are uncertain. The giants, (*Dinichthys*, fig. 123, *Titanichthys*) can be compared with *Coccosteus*, but not so readily with modern Dipnoi.

TETRAPODA.—The Tetrapod skull differs considerably from that of fishes. With rare exceptions it is movable on the vertebral column, the base of the cranium having one (most Sauropsida) or two (Amphibia, Mammals) faces (**occipital condyles**) which articulate with the first (atlas) vertebra, a condition paralleled in fishes only in a few Elasmobranchs. The pterygoquadrate apparatus is more intimately connected with the cranium than is common in fishes; the connexion may even be fusion of more or less of this cartilage, or of the bones (pterygoid and quadrate) which ossify in it, with the cranium, so-called autostyly. Usually the pterygoid part forms but a single bone, but some of the lower Tetrapoda have an **epipterygoid** (**columella cranii**) arising from it. The palatine bone is not connected with the pterygoid cartilage, but arises independently. No Tetrapod has an operculum and all lack distinctly lateral-line canal bones.

Some of the most important differences between fishes and Tetrapoda occur in connexion with the ears. Audition is well developed

in most Tetrapoda, and as most of the species live in the air, the necessity of transmission of sound waves across the middle ear (tympanum) has resulted in the development of a series of ear-bones (**ossicula auditus**) which has an extensive literature. A number of points regarding these are unsettled, but the following statement gives the conclusions of those who have attacked the problems from the ontogenetic and comparative standpoint. Many paleontologists hold views differing in several respects.

All Tetrapoda have an opening (**fenestra vestibuli** *seu* **ovale,** in the lateral wall of the otic capsule, in which is a skeletal structure (**stapes**), preformed in cartilage, (called also 'operculum,' although two other bones have received this name). A process (**stylus**) extends laterally from this basal plate and articulates with one (**Columella,** Amphibia, Sauropsida) or with the first of two (**incus, malleus,** Mammals) more distal elements, the series in either case, ending distally in the tympanic membrane. In Urodeles and Gymnophiona where no tympanic cavity is developed the ossicula are not connected with a tympanic membrane, but in some genera (fig.

FIG. 125.—Diagram of ossicula auditus of (*A*) mammal and (*B*) Sauropsidan. *c*, columella; *e*, Eustachian tube; *fv*, fenestra vestibuli; *i*, incus; *m*, body of malleus; *pi*, internal process of columella; *s*, stapes and stylus; *tc*, tympanic cavity; *tm*, tympanic membrane.

131) the stylus articulates with the quadrate.[1] In all except these and the mammals, the distal element is the **extracolumella** or **hyostapes**; several parts are distinguished in it. The mammalian ossicula auditus will be described in connexion with that group.

The homology of the stapes is uncertain, but the mass of evidence—its position posterior to the seventh nerve, its formation close to, but independent of the otic capsule, and its chondrification from the same blastema as the ceratohyal—goes to show that it is the homologue of the piscine hyomandibula, an element otherwise lacking in Tetrapoda.

AMPHIBIA.—The skull of the lowest Amphibia, the extinct Stegocephala, is very primitive and was used as the basis of the

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[1] Apparently Urodeles have two distinct plates in the vestibular fenestra, one, the stapes, formed lateral to and independent of the otic capsule, from the same stroma which forms the hyoid arch. The other arises posterior to this by segregation from the capsule itself.

general account of the bones of the skull (p. 68). In the existing Amphibian orders, while many primitive features persist, there is considerable modification and even degeneration. Nothing is known of the chondrocranium of Stegocephals; in other groups it largely persists in the adult, and in all the tenth nerve is the last to leave the cranium, a marked contrast to the Amniotes with twelve cranial nerves, and even to Elasmobranchs and many Teleosts where spino-occipital nerves pass through the cranial walls. The Amphibia are poor in cartilage bones, their number being less than in most Teleosts and paralleled, among Ichthyopsida, by some Ganoids and Dipnoi. With this poverty of cartilage bones, the skull is largely a structure of membrane bones and cartilage, the former numerous in Stegocephals, fewer, both by fusion and by absolute loss, in the living groups (*Cf.* figure 126, where lost dermal bones are stippled).
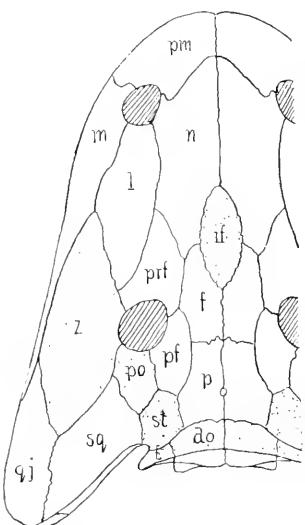
Fig. 126.—Cranium of *Eryops* (Gregory, '20); bones lacking in recent Amphibia stippled. *do*, dermoccipital; *f*, frontal; *if*, interfrontal; *l*, lacrimal; *m*, maxilla; *mm*, manubrium of malleus; *n*, nasal; *p*, parietal, *pf*, postfrontal; *po*, postorbital; *prf*, prefrontal; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal· *t*, tabulare, *z*, zygomatic. (The zygomatic of Caecilians is probably a post-orbital.)

The general features of the cartilage skull are, first, its platybasic character, the cranial cavity extending to the ethmoid region, with no interorbital septum. The notochord, which reaches the hypophysial fenestra, is bordered on either side by a parachordal (often fenestrated) which joins the otic capsules. Each capsule has large foramina on the medial side for vessels and nerves, while the lateral side has the vestibular fenestra. Two postotic vertebræ enter the occipital region, the posterior just behind the vagus nerve. A synotic tectum may arise from upgrowths from otic capsule and vertebræ, but usually there is no roof in front of this until the ethmoid region is reached, the fontanelle being enormous. The prechordal parts, which appear before the chordal, consist of trabecula and sphenolateral developing as a continuum, the latter part forming the 'trabecular crest,' the nerve foramina indicating the line between the two elements in the orbital region. Posteriorly the crest connects with the otic capsule by a process dorsal to the exit of the V–VII nerves (foramen lacerum).

The fenestra hypophyseos is very large at first, later it is closed by cartilage in Anura, but not in Urodeles and Gymnophiona. The floor of the nasal capsule is formed by the trabecular cornua and growth from the ethmoid plate. It is

bounded behind by the antorbital process, its roof formed by growth from the other parts. Internally it is complicated by structures separating the olfactory and vomero-nasal (Jacobson's) organs, the latter known in no fishes, but common in Tetrapoda.

The pterygoquadrate is reduced in most Urodeles, less so in Gymnophiona and least in Anura. Except in Gymnophiona the quadrate part connects with the otic capsule by otic and basal processes, while most Urodeles have an epipterygoid (ascending) process from quadrate to trabecula, dividing the foramen lacerum into two foramina for the fifth and seventh nerves respectively. The relations of the pterygoid process are more primitive in Anura than in the others, as it reaches and fuses with the anterior cranial wall at about the level of the ethmoid region. In Gymnophiona, so far as known, it does not extend so far, while in Urodeles (*Ranodon* and larval *Cryptobranchus* excepted) it is practically undeveloped, at least in the larvæ. Hence the autostyly of Anura is the more primitive, the others cases of degeneration.

The Meckelian cartilage needs no description. There are a hyoid and at most four gill-arches (the fifth branchial possibly being represented in the laryngeal cartilages). The hyoid arch is the largest, the others diminishing in size successively and undergoing more or less change at metamorphosis. At most only the hyoid and first two branchial arches are connected by copulæ, the arches farther back being connected directly to those in front. The parts of the arches are few, the hyoid having cerato- and hypohyal, the gill-arches cerato- and hypobranchial which are all but universally present in the adult.

The striking features of the adult skull are its great flatness (except in Gymnophiona, where, in correlation with the burrowing
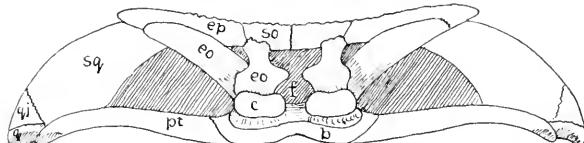
Fig. 127.—Base of cranium of *Mastodonsaurus* (Fraas, '09). *b*, basioccipital; *c*, condyle; *eo*, exoccipital; *ep*, tabulare (epiotic); *f*, foramen magnum; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, dermoccipital; *sq*, squamosal.

habit, it is more cylindrical); the two exoccipital condyles; the all but invariable absence of ossified basi- and supraoccipitals; the firmly fixed (**monimostylic**) quadrate; and in all except Stegocephals, the very great reduction of bones, both in the cranium and the lower jaw, the latter containing, at most, distinct dentale, 'angulare' and splenial (membrane) and a cartilage articulare. The angulare extends forwards on the medial side of Meckel's cartilage, which suggests that it may be a goniale.

STEGOCEPHALIA.—Since development is unknown, the cartilage or membrane character of some bones can be settled only by position

and relations.   The skulls are **stegocrotaphic,** having the temporal
region without fossæ.   A second feature is the large number of
bones and their constancy, points which make these animals impor-
tant for a study of the Tetrapod skull (p. 118).   Some of the bones
are often sculptured or grooved for lateral line canals, the grooves
in some cases forming a well-defined figure (**lyra**) between orbits
and nares.   Viewed from above the skull is triangular, sometimes
elongate, sometimes broader than long.   The nares, far forwards, are
widely separated; the orbits often have a circle of sclerotic bones.
The postero-lateral angles of the cranium are frequently prolonged
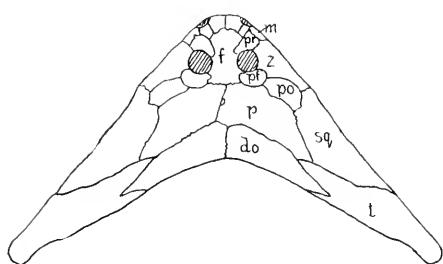
FIG. 128.—Cranium of *Diplocaulus* (Douthitt,
'17).   *do,* dermoccipital; *f,* frontal; *m,* maxilla; *p,*
parietal;   *pf,* postfrontal;   *po,* postorbital;   *pr,* pre-
frontal; *sq,* squamosal; *t,* tabulare; *z,* zygomatic.
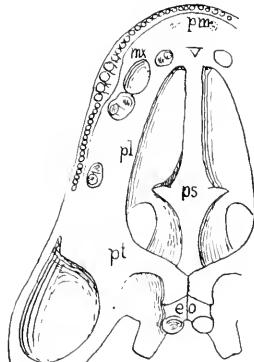
FIG. 129.—Floor of skull of
Eryops (Broili).   *eo,* exoccipital;
mx, maxilla;   *pl,* palatine;   *pm,*
premaxilla; *ps,* parasphenoid; *pt,*
pterygoid.

backwards, leaving a groove (sometimes closed to a fenestra) on the
medial side of each, interpreted as connected with the auditory
apparatus.

   The general relations of the bones of the dorsal surface are shown
in figures 126, 128.   On either side of the middle line at the hinder
end of the cranium is a bone, usually called a supraoccipital, some-
times an interparietal, but it is probably a dermoccipital.   Lateral
to this and reaching to the auditory cleft is a so-called epiotic, but
probably a tabulare.   There is always a parietal foramen between
the parietals; the epiphysial organ which it contained probably was
functional.   In *Eryops* (fig. 126) an **interfrontal** occurs between fron-
tal and nasals, but this is rare elsewhere.   The circumorbital ring is
represented by pre- and postfrontals, postorbital, zygomatic and
lacrimal.   Quadrate and pterygoid are sometimes visible from above,

while supratemporal and squamosal cover the space between parietal and quadrate. The other bones of the roof need no mention other than that on page 120.

The ventral side of the cranium (fig. 129) has at least a pair of large fenestræ, bounded laterally by the anterior end of the ptery-goids, medially by the wall of the cranial cavity. The vomers are usually large, and the parasphenoid extends from them to the base of the skull. All of these bones may bear teeth. A few genera have an **os transversum** intercalated, as in many reptiles, between ptery-goid and maxilla. In the base of the skull the basioccipital is often excluded from the foramen magnum; apparently a supraoccipital never ossifies.

Some genera have the number of bones of the lower jaw reduced as in recent Amphibia; others (fig. 130) have the whole series of the
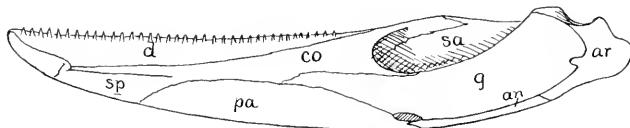
FIG. 130.—Medial side of lower jaw of *Trimerorachus* (Broom, '13). *an*, angulare; *ar*, articulare; *d*, dentale; *co*, coronoid; *g*, goniale; *pa*, preangular of Broom; *sa*, surangu-lare; *sp*, splenial.

more primitive reptiles and fishes. Sometimes (*Archegosaurus*, *Branchiosaurus*) the young, as shown by the fossils, had well-developed branchial arches, some of which are described as bearing teeth, probably similar in function to the gill-strainers (p. 115) of many fishes.

URODELA, whether primitive or neotenic, are most like the Stego-cephals in cranial structure, but with a greatly reduced number of dermal bones, the loss being greatest in forms like *Necturus* and *Proteus* (fig. 134) which have resumed a purely aquatic life. The Urodele chondrocranium has been studied in several species and the following outline gives its salient points, features common to all Amphibia (p. 110) being largely omitted.

The early formed basal plate includes the centrum of an occipital vertebra which at first is separate from the rest of the cranium. The plate is fenestrate later by resorption of cartilage. In *Necturus* the sphenolateral cartilage arises apart from the trabecula, fusing with it later and forming the trabecular crest. The otic capsules arise independently of the basal plate, joining it later, the seventh nerve passing through or beneath the floor of the capsule; the tenth

between capsule and the occipital vertebra, the arch of which soon meets the
capsule above the nerve, completing the jugular foramen. The capsule is
divided internally for the semicircular canals. The relations of the stapes to
the fenestra has been alluded to (p. 119).

The large fenestra hypophyseos may be increased later by resorption of the
cartilage separating it from the openings in the basal plate, so that a common
basicranial fenestra results. The two trabeculæ do not meet in front at first,
but later their union forms the ethmoid plate, beyond which they continue as
the cornua trabecularum beneath the otic capsules. The ethmo-nasal region
differs in the various genera, details of which must be sought elsewhere. The
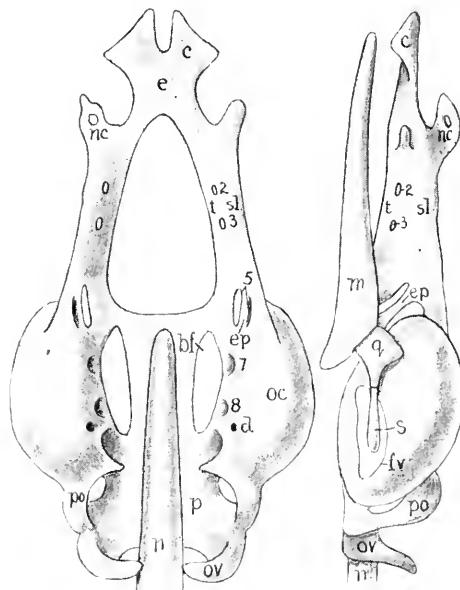
FIG. 131.—Chondrocranium of *Amphiuma*. *c*, cornu trabeculæ; *bf*, basal fenestra;
d, endolymph duct foramen; *e*, ethmoid plate; *ep*, epipterygoid; *fv*, fenestra vestibuli;
m, Meckel's cartilage; *n*, notochord; *oc*, otic capsule; *p*, parachordal; *po*, postotic pillar;
q, quadrate; *s*, stapes; *sl*, sphenolateral; *t*, trabecula; 2–8, nerve exits.

capsules of the two sides are separated in front by an internasal space, while
farther back is a septum, differing in several respects from that of other Verte-
brates. Internally the capsules largely lack the projections which, in higher
groups, are indicative of complication of the olfactory membrane.

The visceral arches (six at most) appear in order, from in front backwards.
The mandibular arch divides at chondrification into pterygoquadrate and
Meckelian. The former part, at first almost entirely quadrate, soon joins the
trabecular wall by the epipterygoid process and later basal and otic processes
connect it with basal plate and optic capsule. The skull thus becomes moni-
mostylic, the monimostyly, like that of Dipnoi, being effected by cartilage union,
and differing from that of reptiles where fixation of the quadrate is largely by

membrane bones. The pterygoid process grows from the anterior side of the quadrate, but, with the exceptions noted on p. 121, it ends freely in front. The Meckelian cartilages of the two sides are separate in front at first, but are continuous cartilage later. At most there are four branchial arches, the posterior two being more rudimentary or even absent. Each arch has not more than two parts, usually called cerato- and hypobranchial (sometimes regarded as epi- and ceratobranchial). Not infrequently the upper ends of the ceratobranchials of the several arches are fused. The copular series often continues behind the attachment of the arches. The arches themselves undergo considerable changes at metamorphosis, the Perennibranchs being the most conservative in this respect.
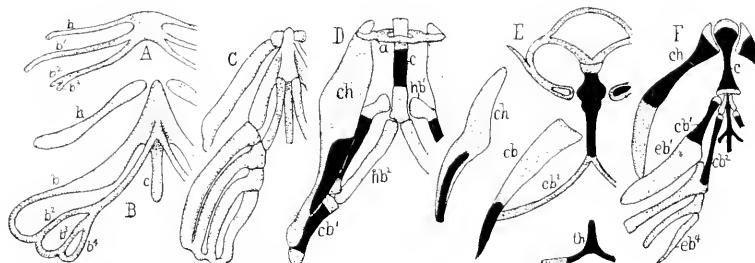
FIG. 132.—Hybranchial skeletons of Urodeles. *A*, *B*, *Triton cristatus* (Stöhr, '77); *A*, embryo 7 mm. long; *B*, 10 mm. *C*, *D*, *Triton taeniatus* (Gaupp, '05); *C*, larva 20 mm.; *D*, after metamorphosis; *E*, adult *Amblystoma punctatum*; *F*, adult *Proteus* (Wiedersheim, '77). Cartilage stippled, bones black.

The adult Urodele skull is more degenerate than that of other Amphibia, as shown by the small number of both cartilage and dermal bones. There is usually no circumscribed temporal fossa, there being no connexion between maxillary and squamoso-temporal regions.[1] The cartilage bones include a pair of exoccipitals bearing condyles. These bones are usually separated by cartilage above and below, no basi- or supraoccipitals ossifying, but they fuse above the foramen magnum in a few genera, and occasionally below it. A pro-otic, the only ossification in the otic capsule, forms in the anterior cupula and extends back on the ventral surface of the capsule, fusing, except in Perennibranchs, with the exoccipital, the resulting bone being usually called the **petrosal,** though differing from the mamma-lian petrosal. In the interorbital region are two (primitively) paired bones extending forwards to the nasal region and usually including the optic foramen, hence they are orbitosphenoids, though often

[1] In *Ranodon* and the larva of *Cryptobranchus* the pterygoid cartilage is continuous with the anterior chondrocranial wall. In *Anaides* it reaches the maxilla. *Diemictylus* and *Triton* have a fossa bounded laterally by a bar from the postfrontal which meets the squamosal behind.

called **sphenethmoids**; but there is some uncertainty here. The columella is usually cartilage through life, but stapedial plate and stylus may ossify separately. The pterygoquadrate is usually ossified in part, but the pterygoid process remains cartilage, a membrane bone (also called pterygoid) developing on its ventral
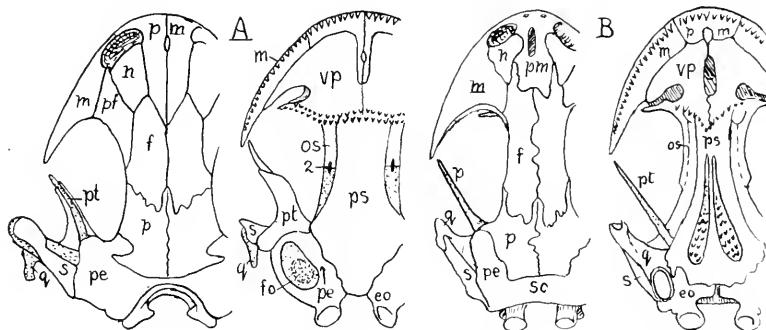
Fig. 133.—*A*, Cranium of *Amblystoma punctatum; B*, of *Desmognathus fuscus* (Wiedersheim, 77). *eo*, exoccipital; *f*, frontal; *fo*, fenestra ovale; *m*, maxilla; *n*, nasal; *os*, orbitosphenoid; *p*, parietal; *pf*, prefrontal; *pm*, premaxilla; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, squamosal; *vp*, vomero-palatine.

surface except in Derotremes and those Salamandrines with teeth on the parasphenoid. The quadrate is overlaid by the squamosal, these two, directed downwards and forwards, suspending the lower jaw, the hinge being far forwards, in some species even at the middle of the skull. In some the stylus articulates directly with the quad-
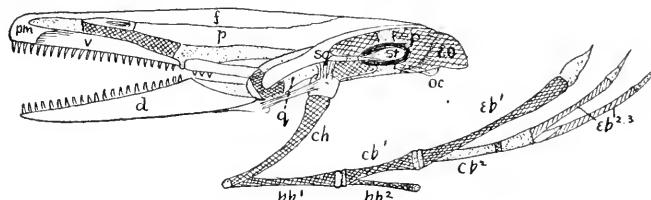
Fig. 134.—Skull of *Proteus* (Wiedersheim, '77). *bb*, basibranchial; *ch*, ceratohyal; *d*, dentale; *ep*, epibranchial; *eo*, exoccipital; *f*, frontal; *p*, parietal; *pm*, premaxilla; *q*, quadrate; *sq*, squamosal; *st*, stapes; *v*, vomer; cartilages stippled.

rate, an important point in considering stapedial structures as possible homologues of the hyomandibula.

The roofing bones of the cranium include parietal, frontal, usually nasal, and sometimes a prefrontal (Parker's ectethmoid) on either side, the latter bone forming the anterior border of the orbit. Rarely (*Ellipsoglossa, Ranodon*, etc.) another bone, now interpreted as

lacrimal, may occur in front of the prefrontal. The parietal has a descending postorbital process which (*Necturus*) may meet the parasphenoid. The frontals extend from the parietals to the nasal region. Posteriorly the squamosal (**paraquadrate, 'tympanic'**) extends from the parietal over the dorsal side of the otic capsule and the quadrate, nearly to the hinge of the jaw. Many genera (Plethodontidæ, Amblystomidæ) have a septomaxillary, traversed by the lacrimal duct, developed in the membrane of the nasal capsule. The tip of the cranium is formed by a pair of premaxillæ (fused in *Amphiuma*) which send processes back to meet the frontals. The rest of the margin of the upper jaw is usually formed by the toothed maxillæ, but Perennibranchs lack maxillæ.

A large parasphenoid (developing late) occupies the middle of the roof of the mouth and is toothed in many genera, and in so-called Lechriodonts both vomers and palatines may bear teeth, the two bones of a side frequently fusing to a **vomero-palatine** plate. The membranous pterygoid (p. 126) also enters the oral roof and in some genera meets the palatine. Those Lechriodonts with toothed parasphenoid lack a pterygoid bone.

The only cartilage bone in the lower jaw is the articulare, except in *Proteus*, said to have a mentomeckelian. Most of the jaw is formed by membrane bones—dentale, angulare, and sometimes a splenial—the 'angulare' (possibly goniale, p. 121) may fuse with the articulare. There are few ossifications in the hyo-branchial skeleton. The most primitive are the Perennibranchs and the larvæ of other forms. Fusion of the dorsal ends of the arches of a side is common. The number of arches persisting in the adult (fig. 132) ranges from two (Salamandrina) to four (Perennibranchs and Derotremes). The hyoid has cerato- and hypohyal parts. Hyoid and first branchial arch are connected by a basihyal, scarcely distinct from the middle part of the copula farther back. The other arches are connected with the hyobranchial of the arch in front. Many Salamandrina have an arcuate bar (fig. 132, *E*) in the floor of the pharynx in front of the hyoid which connects the cornua of the two sides. Another peculiarity is the separation in these same forms of the posterior part of the copular apparatus as a distinct bone (**os thyreoideum** or **triquetrum,** figure 132, *E*), lying just ventral to the pharynx and in front of the pericardium.

Fossil Urodeles are rare. *Lysorophus* (fig. 135) from the Permian is apparently one, having the general Urodele structure except a median bone behind the parietals, which is without parallel in modern Amphibia. The stegocrotaphic skull suggests the Gymnophiona, but details oppose such association. The four branchial arches and the exoccipital condyles exclude it from the Reptilia, though Broili regards it as reptilian because of the participation of the basioccipital in the condyles.

GYMNOPHIONA.—The skull of the Cæcilians recalls with its almost stegocrotaphic roof, the Stegocephals, but there is less resemblance in details. There is a gap, small in *Ichthyophis* and *Cæcilia*, larger in
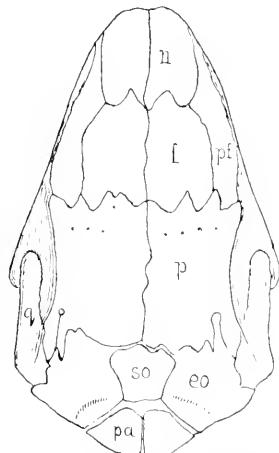
FIG. 135.—Skull of *Lysorophus* (Williston, '08). *eo*, exoccipital ; *f.* frontal; *n*, nasal; *p*, parietal; *pa*, ?proatlas; *pf*, prefrontal; *q*, quadrate; *so*, possible supraoccipital.
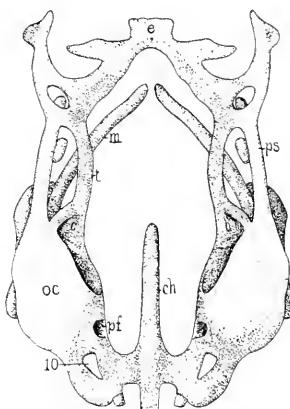
FIG. 136.—Chondrocranium of *Ichthyophis* (Winslow, '98). *ch*, notochord; *e*, ethmoid plate; *oc*, otic capsule; *pf*, perilymph foramen; *ps*, sphenolateral; *t*, trabecula.

Siphonops, between parietal and postfrontal; the bones are fewer than in Stegocephals. Unfortunately no fossils are known; the recent species are tropical.

The chondrocranium (only the later stages known) is more Urodelan than Anuran (fig. 136). The large basicranial fenestra is traversed behind by the notochord which is absorbed later. The otic capsule is nearly closed medially. Trabecula and sphenolateral are more distinct than in other Amphibia, the ethmoid plate formed by union of the trabeculæ is farther forwards, relative to the nasal capsules, than is usual in Amphibia. The pterygoquadrate is small, the larger quadrate part bearing pterygoid and epipterygoid processes, the former not reaching the cranium in front. The quadrate resembles that of Urodeles in its downwards and forwards direction and its articulation with the stapedial stylus. The Meckelian cartilage is noteworthy for the distance it

extends behind its articulation with the quadrate. There are four gill-arches, persisting as cartilage in the adult, while the copula extends forwards as a sort of entoglossum.

The adult skull has few cartilage bones. Exoccipitals and prootics soon fuse with each other and with the large parasphenoid, forming a large **basal bone** which extends forwards on the ventral surface to the vomers, while dorsally the occipito-petrosal part is visible at the base of the skull. A characteristic is the ethmoid (lacking in Urodeles) apparently composed of ect- and mesethmoidal parts, the mesethmoid appearing in some genera between the frontals, while ectethmoid parts are visible on the palatal surface of *Ichthyophis*. There are no otic or basal processes to the quadrate; articulare and angulare are usually fused.
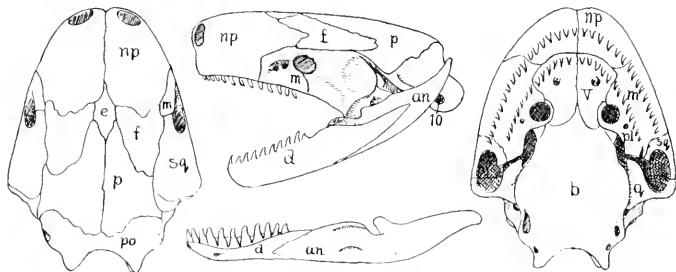
FIG. 137.—Skull of *Siphonops annulatus* (Wiedersheim, '79). *an*, angulare; *b*, basale; *e*, 'ethmoid;' *f*, frontal; *m*, maxilla; *np*, naso-premaxilla; *p*, parietal; *pl*, palatine; *po*, petroso-occipital; *q*, quadrate; *sq*, squamosal; *v*, vomer.

The homologies of some membrane bones are uncertain. Parietals, frontals, nasals and premaxillæ need no mention further than to say that the latter two fuse in Siphonops. In or near the anterior margin of the very small orbit is a prefrontal and adjacent to this a small septomaxillary (called turbinal and lateral nasal) is visible in some from above; it may fuse with the nasal. The suspensor of the lower jaw is probably quadrate and squamosal, the latter on the dorsal side. Between it and the maxilla the margin of the cranium is formed by a membrane bone (fig. 138, *pf*), called jugal, zygomatic and squamosal, but which development suggests is a postfrontal. In the maxilla, or between it and the premaxilla, is the foramen for the tentacular apparatus characteristic of the order. *Ichthyophis* has a small bone above the orbit, probably a supraorbital.

The large basale on the ventral surface has been mentioned. Palatine and maxilla fuse, both elements bearing teeth as does the

9

anterior border of the vomer. In the lower jaw angulare and articulare fuse as do dentale and splenial. The angulare extends back over the posterior process of the Meckelian. Some genera have
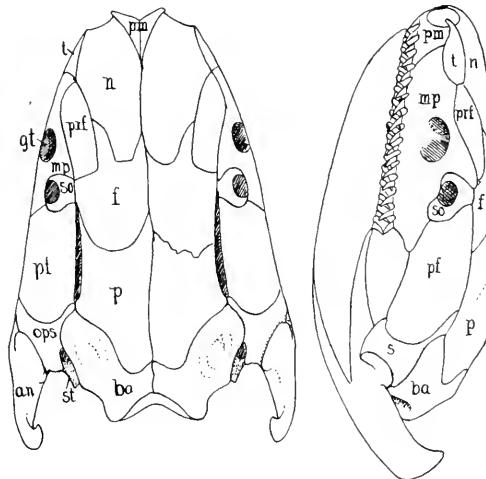
FIG. 138.—Skull of *Ichthyophis* (Sarasins, '90). *an*, angulare; *ba*, basal; *f*, frontal; *gt*, groove for tentacle; *mp*, maxillo-palatine; *n*, nasal; *ops*, otic process of suspensorium; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla. *prf*, prefrontal; *so*, supraorbital; *st*, stapes; *t*, Sarasins' turbinal (septomaxillary).

teeth which are apparently both dentary and splenial in origin. The other visceral arches of Cæcilians (fig. 139) are greatly simplified or even degenerate when compared with those of other Amphibia.
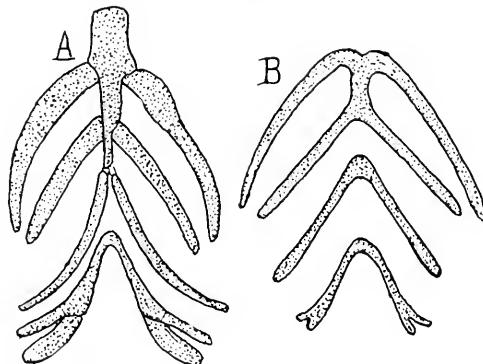
FIG. 139.—Hyobranchial skeletons of *Epicrium* (Sarasins, '90). *A*, of larva; *B*, adult.

ANURA, although usually regarded as higher than Urodeles or Gymnophiones, have a skull more primitive in many respects, this appearing especially in the more complete retention of the chondro-

cranium, the complete pterygoid and zygomatic arches, the latter bounding a temporal fossa, and in the presence of a quadratojugal bone.

The chondrocranium is more fully developed than in other Amphibia, and at metamorphosis it undergoes extensive modifications, probably correlated with changes in food, the tadpole (larva) scraping minute vegetation from submerged objects with the horny jaws of the small mouth, the carnivorous adult bolting large objects. As a result of the food, the prechordal parts are first to appear (fig. 140). There is no cranial flexure, the trabeculæ lying in the plane of the notochord, and extending forwards to meet a **suprarostral plate** on either side (possibly the homologue of the upper labial of Elasmobranchs), which supports the horny jaws and appears before parts farther back. Behind this plate the trabeculæ meet in an ethmoid plate. When parachordals and otic capsules are outlined, the trabeculæ join the basal plate arising from the former, enclosing a large fenestra hypophyseos.

FIG. 140.—Early chondrocranium of *Rana* (Stöhr, '81). *ct*, trabecular cornu. *e*, ethmoid plate; *ep*, epipterygoid; *n*, notochord; *p*, parachordal; *pq*, pterygoquadrate.

The jugular foramen is completed by the junction of the pillar-like occipital vertebra with the otic capsule and about the same time a sphenolateral bar (**tænia marginalis**) arises in the interorbital region, uniting with both trabecula and otic capsule, thus completing the foramen lacerum for the V, VI and VII nerves. Later, the floor of the cranial cavity is completed by growth from the surrounding parts, while additions are made to the side walls from the anterior end of the sphenolateral and also from where

FIG. 141.—Chondrocrania of *Rana. A*, larva with tail disappearing (Parker, '70); *B*, just after metamorphosis (Gaupp, '93). *al*, alary cartilage; *c*, trabecular cornu; *e*, epipterygoid; *et*, ethmoid region; *fv*, fenestra vestibuli; *l*, lower labial; *m*, Meckelian; *oc*, otic capsule; *pq*, pterygoquadrate; *pt*, pterygoid; *q*, quadrate; *s*, stapes; *t*, trabecula; *tm*, median tænia; *tn, ts*, tectum of nasal and synotic regions; *tp*, terminal plate of nasal capsule.

the pterygoquadrate joins the cranium in front. The roof is never complete, but in older larvæ a transverse bar is connected with the synotic tectum by a median cartilage, these parts separating a pair of fenestræ from a larger anterior fontanelle. The complicated nasal capsules need not be described here.

The pterygoquadrate arises apart from the chondrocranium, but soon becomes connected with it by an epipterygoid bar behind, and in front by fusion a little behind the nasal capsule. It rapidly increases in size, extending forwards nearly to the suprarostral, the small Meckel's cartilage being articulated to it far forwards, and coming into close relations with a small **infrarostral cartilage** (probably a lower labial), which supports the horny lower jaw. At metamorphosis the articulation of the lower jaw shifts (in a way not easily described) from near the anterior end of the pterygoquadrate to a point behind the epipterygoid, thus greatly increasing the gape of the mouth. During metamorphosis the infrarostrals join the Meckelians, eventually ossifying as a mento-meckelian on either side. The suprarostrals are lost. A cartilage tympanic annulus to support the tympanic membrane becomes closely related to the lateral side of the tympanum.

The cartilage bones of the adult include the pairs each of exoccipitals, prootics, stapedial structures, ethmoids (paired in ossification) and the articulare parts of the pterygoquadrate. (In some of these ossification is not complete.) The ethmoid (**sphenethmoid,** alisphenoid, **os en ceinture,** 'girdle bone') begins as a pair of ossifications close to the olfactory foramen and never extends back so as to include the optic nerve, excluding an alisphenoid homology. The prootics ossify in the anterior cupula and extend thence into basal and trabecular cartilages as well as to the other sides of the otic capsules. The exoccipitals are separate and always bear a pair of occipital condyles.

Each parietal, which covers part of the otic capsule, fuses early with the frontal of the same side to a **fronto-parietal bone** which reaches to the ethmoid, while behind it meets the exoccipital. The nasal lies obliquely over the nasal capsule, a gap existing between it and the ethmoid behind and the premaxilla in front. No prefrontal occurs. A septomaxillary develops in the nasal region behind the naris and covers the opening of the lacrimal duct, a part of which is more or less completely enclosed in the bone. The squamosal (separated from the parietal by the prootic which appears on the surface of the skull) is three-branched, the lateral ramus entering the hinge of the jaw, the anterior extending forwards above the pterygoquadrate (subocular) bar and in some genera may meet the maxilla. The slender maxilla connects behind with a bone (usually called the quadratojugal, but as it includes material derived from the pterygoquadrate has been called a **quadratomaxillary**) completing an arch like the zygomatic of other Vertebrates. although it contains no zygomatic bone.

The roof of the mouth, which has a large vacuity on either side, is most formed by a large parasphenoid, the first bone to ossify in the skull. It is expanded behind, a process extending to either otic region; its anterior end covers part of the ethmoid, and on either side of its tip is a slender palatine bone in a transverse position,
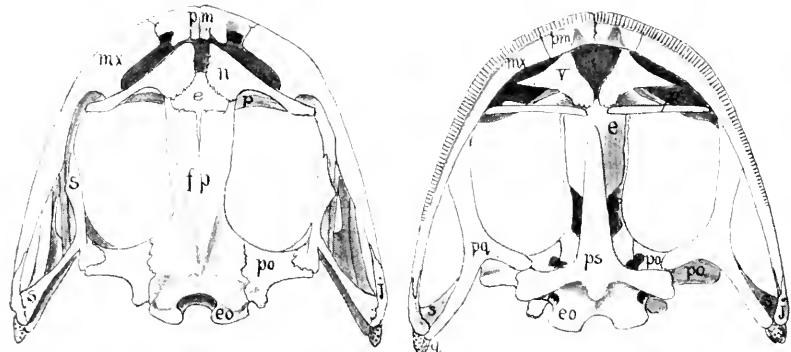
FIG. 142.—Dorsal and ventral sides of skull of *Rana catesbiana.* *e,* ethmoid; *eo,* exoccipital; *fp,* frontoparietal; *j,* quadratojugal; *mx,* maxilla; *n,* nasal; *p,* palatine; *pm,* premaxilla; *po,* prootic; *pq,* pterygoid overlying pterygoquadrate; *ps,* parasphenoid; *q,* quadrate cartilage; *s,* squamosal.

reaching to maxilla and pterygoid. The toothed vomers in front of the palatine are small. As in other Tetrapoda the pterygoid bones are membranous in origin. Each reaches the maxilla and palatine in front; one of its posterior processes extends to the para-

FIG. 143.—Development of hyobranchial apparatus of *Rana* (Stöhr, '81, and Gaupp, '05). *A,* 9 mm. larva; *B,* 29 mm. larva; *C,* end of metamorphosis; *D,* adult (Gaupp, '96). *ac,* anterior cornu; *b,* branchial arches; *c,* copula; *cb,* ceratobranchial; *ch,* body of hyoid; *h,* hyale; *hc,* hyoid cornu; *th,* 'thyreoid process.'

sphenoid, the other runs postero-laterally on the ventral side of the quadrate, parallel to one of its branches.

The suspensor of the lower jaw, formed of quadrate, squamosal and pterygoid, is directed backwards and downwards, carrying the

angle of the mouth far back.   The articulare persists as cartilage
partly enclosed by the angulare, while farther in front the toothless
dentale envelops the anterior part of Meckel's cartilage.   The tip
of the lower jaw is formed by the mentomeckelian already
mentioned.

The hyobranchial cartilages (hyoid and four branchials) develop
in order from in front backwards.   At first (fig. 143, *A*) the hyoid
and first gill arch are continuous, the others separate.   The medial
ends of all the arches next fuse to a hypobranchial plate (*B*), the
copula between hyoid and the first gill-arch probably being basi-
branchial.   At metamorphosis some parts are reduced, others
increased; the lateral ends of the hyoid extend as the cornua (*C*),
while hypobranchial and copular plates fuse.   The adult (*D*) has a
large median plate, the hyoid body, bearing the long cornua which
are connected with the otic capsule, while behind are two posterior
cornua which contain the only ossifications, and which are said, in
Rana, not to be a part of the branchial arches, although this is
affirmed for some Anura.

AMNIOTA must have had a common origin, but, as shown by
the large number of cranial bones, they cannot have come from any
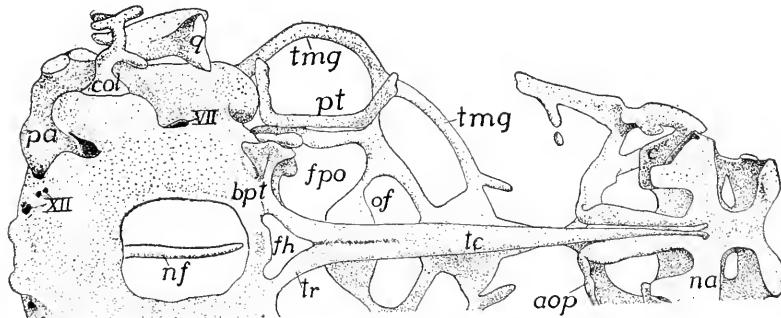
Fig. 144.—Chondrocranium of *Lacerta* (Gaupp, '00). *aop*, antorbital plate;
bpt, basipterygoid process; *c*, entrance to nasal conch; *col*, columella; *fh*, fenestra
hypophyseos; *fpo*, postoptic fenestra; *na*, nasal capsule; *nf*, notochord; *of*, optic foramen;
pa, posterior ampulla; *pt*, pterygoid; *q*, quadrate; *tc*, trabecula communis; *tmg*, marginal
tænia; *tr*, trabecula; VII, XII, nerve exits.

existing order of Amphibia, but must have had a Stegocephalian
ancestry, which may have been the diverging point of Sauropsida
and Mammalia; or this separation may have occurred after the
appearance of the Theromorphs, there being evidence in favor of both
views.

Among the characteristics of the Amniote chondrocranium, so far as known, are its tropibasic structure (fig. 144), the paired trabeculæ uniting to a trabecula communis just in front of the hypophysis, leaving a small hypophysial fenestra. To accommodate the greatly enlarged lagena of the ear, this organ has invaded at least the basal plate. The nasal capsule is more complicated, one feature being the paraseptal cartilages, primarily connected with the floor of the capsule and protecting the vomero-nasal organ. The pterygoid arch is reduced, never reaching the nasal capsule. The roof of the cranium is reduced to the synotic tectum and the occipital region. The branchial arches, in correlation with the loss of branchial respiration, are reduced and modified for other functions, and some arches are entirely lost.

In the adult skull may be noted the ossification of basi- and supraoccipital, and also a basisphenoid, unknown in Amphibia, while the parasphenoid, so large in Amphibia, is greatly reduced or even lost. When present it is usually fused with the basisphenoid or presphenoid, when apparently lost, some maintain (p. 77) it to be represented by the vomer. Another feature is the suspensor of the lower jaw, which, as shown by Teleostomes, was originally movable on the cranium (**streptostylic**). This condition exists in Squamata and birds (probably secondary) and in mammals where the homologue of the quadrate (**incus**) is free, although its suspensorial function has gone. All other reptiles (Monimostylica) have an immovable quadrate, it being fixed by the squamosal and frequently by other bones.

There is also a reduction and fusion of some of the visceral arches, some contributing to the hyoid apparatus, in which three arches at most are concerned, while there is a probabili˙y that the hyoid has contributed to the ossicula auditus (p. 119). The more posterior arches may take part in the laryngeal and bronchial cartilages. The hyoid apparatus is ventral to the larynx, and in many groups, in contrast to the Ichthyopsida, it supports a true tongue.

SAUROPSIDA.—Among features common to the skulls of both reptiles and birds are: 1, the lack of a chondrocranial roof aside from the synotic tectum; an entire independence of the pterygoquadrate cartilage, and often a separation of quadrate and pterygoid parts, the whole bar being weakly developed; 2, a single occipital condyle largely or wholly on the basioccipital, although in the embryo and

sometimes in the adult (as in *Chelonia*) the exoccipitals may con-
tribute to it; 3, the existence, except in snakes and some turtles, of a
high (cartilage or osseous) interorbital septum, continued forwards
as a nasal septum; 4, as a result, the cranial cavity is restricted to the
postorbital cavity and the presphenoid is reduced; 5, the large
number of distinct bones appearing in development, especially in
the orbital and temporal regions and the frequent occurrence of
sclerotic bones.

There are two lines of cranial structure in Sauropsida, strepto-
stylic and monimostylic. The former includes only Squamata and
birds; the latter all other orders, living and extinct. In the latter
the quadrate is held firmly by the squamosal and other bones; in
the streptostylic group the quadrate moves freely on the cranium,
this mobility often extending to the pterygoids (which do not meet
in the median line) and occasionally (some birds) to the anterior part
of the cranium. The number of bones appearing in development is
greater than in mammals or existing Amphibia, but the number is
often reduced in the adult by fusion, especially in birds.

REPTILIA.—The skull of most reptiles differs from that of
birds in the greater number of bones in both young and adult. The
relations of the foramen magnum are more primitive in reptiles in
being directed backwards instead of downwards, Pterosaurs forming
an exception to this general statement. As a result of the smaller
brain, the reptilian otic capsules form a part of the lateral cranial
wall, instead of its floor, while the squamosal, in all lower groups is
excluded from the wall of the cranial cavity.

As in all Amniotes, the chondrocranium (fig. 144) is distinctly
tropibasic. The trabecula communis passes dorsally into inter-
orbital and nasal septa, and in front to structures comparable to the
trabecular cornua and ethmoid plate of Ichthyopsida. The inter-
orbital septum separates dorsally as a pair of supraseptal plates
(fig. 68) which lie immediately below the olfactory nerves. The
basal plate may be entire or may have one or more basicranial fenes-
træ, the lagenar part of the ear extending into it. The chondro-
cranial roof is poorly developed, there being a narrow synotic tectum
sometimes with a narrow bar extending forwards from it.

The preotic parts are relatively lighter, more slender and more
complicated than in Ichthyopsida, the lateral walls in front of the
otic capsules being reduced to one or more bars (an upper marginal

tænia and a lower **middle parietal tænia**) in place of the sphenolateral, and having large fenestræ between them. Between the orbits these tæniæ meet in the interorbital septum, diverging dorsal to the eyes as the **supraseptal plates.** The nasal capsules are complicated internally. Usually there is an epipterygoid process, but this never fuses with the cranium. The visceral arches are reduced, the posterior being small or absent.

The skull of the most primitive reptiles (Cotylosaurs, figure 152) is like that of Stegocephals in the numerous bones of the roof and in the stegocrotaphic condition; nares, orbits and parietal foramen being the only openings in it. (The somewhat similar roof of the Chelonians is probably secondary in character.) Except in the
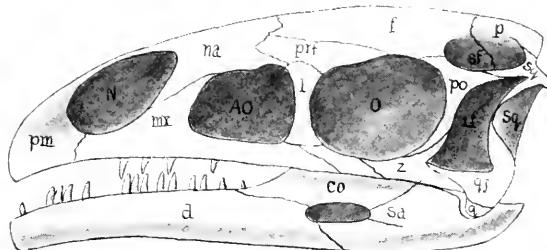
Fig. 145.—Skull of *Plateosaurus* (Fraas, '11). *AO*, antorbital vacuity; *co*, coronoid; *d*, dentale; *f*, frontal; *if*, infratemporal fossa; *l*, lacrimal; *mx*, maxilla; *N*, naris; *na*, nasal; *O*, orbit; *pm*, premaxilla; *po*, postorbital; *prf*, prefrontal; *q*, quadrate; *qj*, quadrato-jugal; *sa*, surangulare; *sf*, supratemporal fossa; *sq*, squamosal; *z*, zygomatic.

Cotylosaurs and Chelonia there are one or more pairs of gaps (fossæ) in the roof, the more common condition being with both supra- and infratemporal fossæ (fig. 145), these differing considerably in size, being very large in Squamata, Ichthyosaurs and Pterosaurs. Sometimes a posttemporal fossa is present.

The infratemporal fossa is bounded laterally by a bar (arcade) of the zygomatic processes of squamosal and zygomatic bones, the quadratojugal usually intervening between the two. Medially it is separated from the supratemporal fossa by a second arcade, usually formed of squamosal and postorbital, but postfrontal and even zygomatic may enter it. Usually the posttemporal fossa lies between parietal, supratemporal and exoccipital or opisthotic bones. The lower arcade is always lacking in Squamata, only the supratemporal fossa being complete. Again, interruption of the upper arcade results in a single temporal fossa, and then the absence of the lower

arcade, as in snakes, results in the disappearance of all vacuities, in snakes probably the result of the looseness of the squamosal and the great mobility of the quadrate. Usually the fossæ are separated from the orbit by an ascending orbital process of the zygomatic which meets the bones (postorbital, postfrontal, when these are present) which bound the orbit behind, but when these are absent, the orbital process usually extends to the frontal. In some fossil reptiles (Theromorphs, Dinosaurs, Pterosaurs, figures 145, 180) there may be vacuities in front of the orbit.

The history and probable genealogy of the temporal fossæ have been the basis of several theories. One is that the supratemporal fossa arose by an extension forwards and closure behind of the so-called auditory notch of many Stegocephals (fig. 76) and *Seymouria* of the Theromorphs, but this does not seem probable. Another view of the homologies concerned is shown in figure 79. The fossæ and their arcades have been used in dividing Reptilia into two groups, Synapsida and Diapsida. In the first of these (many Theromorphs, Plesiosaurs, Ichthyosaurs, some Chelonians and primitive Crocodilians) there is either a stegocrotaphic cranium or a single fossa bounded medially by parietal and supraoccipital, laterally by postfrontal (sometimes also by postorbital) and squamosal, with below them and forming the ventral side of this arcade, zygomatic and quadratojugal. In later Crocodilia, Rhynchocephalia and Dinosauria the lower arcade is perforated by an infratemporal fossa, the lower boundary of which is formed of squamosal and zygomatic and often the quadratojugal.

All four occipitalia are developed, but in Crocodilia and Ophidia the supraoccipital may be excluded from the margin of the foramen
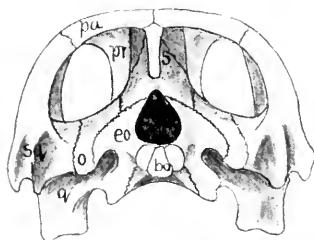
magnum; in snakes and some turtles the basioccipital is crowded out, the foramen occasionally being bounded by exoccipitals alone. The base of the skull articulates with the atlas by a single (median) occipital condyle, largely or wholly (Crocodilia, Ichthyosaurs) formed from the basioccipital, but frequently the condyle is tripartite (fig. 146) the exoccipitals contributing to it, while in some reptiles (some Theromorphs and Chelonians) the basioccipital part is reduced, the exoccipitals alone affording the articular surfaces.

The roof of the cranial cavity is formed almost entirely of frontals and parietals, the former usually the larger and extending to the

ethmoid region. Most of the extinct orders (Dinosaurs and Ptero-
saurs excepted) and Rhynchocephals and lizards have a parietal
foramen for the parietal eye between the two parietals.[1]

The nasals (fused in some lizards and lacking in all Chelonia
except *Chelys* and its allies, figure 147) vary in length with that of the
snout, reaching the extreme in Crocodilia and Ichthyosaurs. Usu-
ally they extend to the nares and form part of the nasal septum, being
met in the median line by the ascending processes of the premaxillæ.
The orbit is bounded by several bones. In front is the more median
prefrontal[2] (in turtles replacing the nasal) and lateral to this in many
lizards is a lacrimal. The posterior border
is composed of postfrontal and usually a
postorbital, the latter occurring in recent
groups only in Squamata and *Sphenodon*.
Lacertilia, Ichthyosaurs, *Python* and some
Dinosaurs may have one or more supra-
orbitals, while some lizards have other
bones on the lower and posterior sides of
the orbit. Several extinct groups (Pyth-
onomorphs, Ichthyosaurs, Plesiosaurs,
some Theromorphs and Pterosaurs) may
have sclerotic bones.

As a rule the lateral margin of the cra-
nium consists of premaxilla, maxilla, zygo-
matic and quadratojugal, the latter
reaching the squamosal, which to a
greater or less extent overlies the quad-
rate at or near the posterolateral angle
of the cranium. In the lower extinct

FIG. 147.—Cranium of *Hydro-
medusa* (Jaekel. '11). *f*, frontal;
l, prefrontal; *m*, maxilla; *n*,
nasal; *oo*, opisthotic; *os*, supra-
occipital; *p*, parietal; *po*, post-
orbital; *pr*, prootic; *pt*, ptery-
goid; *q*, quadrate; *sq*, squamosal;
v, vomer; *z*, zygomatic.

orders a supratemporal often occurs between parietal and squa-
mosal, and behind this, on the posterior margin of the cranium
a **tabulare** (so-called epiotic). The tabulare often appears in the

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[1] Occasionally the parietal foramen is farther forwards in the median line, even
between the frontals. A few Theromorphs have an interparietal bone between the
parietals and the supraoccipital. The parietals are fused in Crocodilia and most
Squamata, the frontals also in the former.

[2] Watson has shown that the lacrimal of *Nythosaurus* and *Diademodon* is so closely
similar to that of *Perameles* (mammal) that Gaupp's contention that the mammal lacri-
mal is the reptilian prefrontal will not hold. Gaupp called the reptilian lacrimal the
adlacrimal.

development of several living reptiles, fusing later with either supra-
or exoccipital. When the supratemporal bone is lacking the squa-
mosal extends to the parietal.

The floor of the cranium is shown in diagram in figure 148.
Beginning behind, in the median line are basioccipital and basisphen-
oid, preformed in cartilage and ossified in the adult. Usually
(Ichthyosaurs, Squamata, Rhynchocephals, Dinosaurs) the basi-
sphenoid is continued forwards by a slender 'rostrum,' apparently
cartilage in origin and representing the presphenoid; it supports the
interorbital septum. The bas-
ioccipital is flanked on either
side by exoccipital and opistho-
tic, the latter meeting the
quadrate at the postero-lateral
angle of the cranium. A ptery-
goid, dermal in origin, extends
forwards from the quadrate,
and in more specialized reptiles
comes into more or less intimate
relations with the basisphenoid,
usually by a **basipterygoid
process** of the latter. Still
farther forwards the pterygoid
series is continued by a (dermal)
palatine, and this, in turn, by a
vomer. In most living groups
an **os transversum** extends from
pterygoid to maxilla. The only
pterygoid element of cartilage
origin is the epipterygoid
(columella cranii) occurring, among recent species, in most lizards
and in *Sphenodon*. It extends from the dermal pterygoid up to the
lower side of the parietal. It was probably present in some Thero-
morphs, Ichthyosaurs and Dinosaurs.
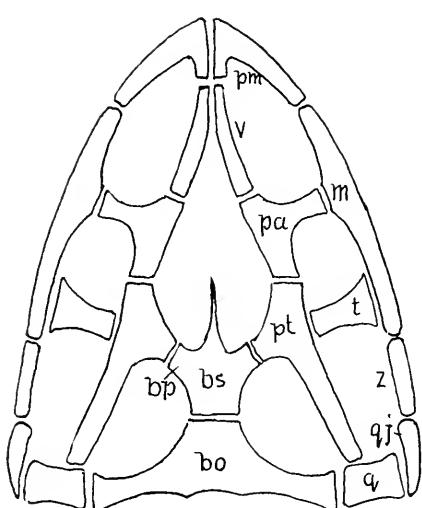
FIG. 148.—Scheme of floor of reptilian
cranium (Butschli, '10). *bo*, basioccipital;
bp, basipterygoid process; *bs*, basisphenoid
and rostrum; *m*, maxilla; *pm*, premaxilla; *pa*,
palatine; *pt*, pterygoid; *q*, quadrate; *qj*, quad-
ratojugal; *t*, transversum; *v*, v o m e r; *z*,
zygomatic.

The rostrum (part of which may be parasphenoid) is smallest in monimostylic
species. The basisphenoid is visible in its whole extent in Squamata, partially
in Chelonia; in Crocodilia it is largely covered by the pterygoids. Chelonia,
Plesiosaurs, Theromorphs and Pterosaurs have no transversum, a bone which
is not the same as the ectopterygoid of fishes as sometimes stated.

There are usually large vacuities between certain of these floor bones, and the position of the choanæ is very variable; usually they are far forwards, the anterior ends of the vomers lying between them, or the choanæ of the two sides are approximate. From this primitive condition all others are derived. Palatal processes from premaxilla may extend medially, passing below the primitive choanæ and cutting off a respiratory duct from the roof of the mouth, so that the definitive choanæ are carried back to the edge of the hard palate thus formed. Then palatines and pterygoids may meet in the same way in the middle line, so that the choanæ are still further back, the extreme occurring in modern Crocodilia (fig. 178) where these openings are near the posterior end of the cranium. This meeting of palatines and pterygoids covers vomers and sphenoids so that they are excluded from the roof of the mouth.

The cranial cavity (fig. 149) is bounded posteriorly by the occipitalia. The otica form its posterolateral walls. Of the otica the exact relations are known in a few groups. Chelonia, *Sphenodon*, and older Crocodilia have a distinct opisthotic; elsewhere it appears in ontogeny,

FIG. 149. — Internal surface of posterior part of cranium of *Alligator* (Pouchet et Beauregard, '89). *as*, alisphenoid; *bo*, basioccipital; *bs*, basisphenoid; *e*, epiotic; *eo*, exoccipital; *fr*, frontal; *f*, hypophysial fossa; *pa*, parietal; *po*, prootic; *oo*, opisthotic; *pt*, pterygoid; *so*, supraoccipital.

fusing later with the exoccipital, forming a **parotic process**; it fuses above with the prootic which forms the anterior wall of the otic capsule. Whether an epiotic be present is questionable, the bone often given that name is the tabulare.

Farther forwards the lateral cranial wall is formed by alisphenoids (lacking in Chelonia and Ophidia) which also form part of the posterior wall of the orbit and extend dorsally to frontal and parietal. In Chelonia the parietal sends a broad process down to the basisphenoid, closing the orbit from the brain cavity. Similar processes from the frontal extend the medial wall farther forwards. Most reptiles have a well-developed interorbital septum (nearly or quite lacking in Chelonia and Ophidia), usually of membrano-cartilage,

but here and there small bones (possibly orbitosphenoidal) may occur in it. Perforation of the septum is common.

Other cranial bones are the septomaxillaries (conchæ, fig. 150), one on either side in the floor of the nasal capsule and between the organ of Jacobson and the nasal septum, these occurring in lizards, *Sphenodon*, Phytosaurs and some Theromorphs, some of the latter having an 'infranasal bone.' Some Orthopodous Dinosaurs have an unpaired 'rostral bone' in front of the premaxillæ.

FIG. 150.—Diagrammatic cross-section of nasal skeleton of snake (Bütschli, '10). *n*, nasal; *s*, septomaxillary; *v*, vomer.

The lower jaw is supported by the quadrate which is connected with the cranium by other bones, most prominent of which is the squamosal, which plays no part here in the cranial wall. It overlaps the quadrate more or less completely behind (the extreme occurring in turtles, fig. 155), either holding it firmly (Monimostylica) or allowing it to play on the cranium (Streptostylica). In most recent reptiles the squamosal articulates with the parietal and often with the parotic process of the exoccipital and opisthotic, the prootic sometimes contributing to the process. Many Theromorphs have a supratemporal. The quadrate itself is large except in most Theromorphs.

Meckel's cartilage often persists in the lower jaw until old age, its posterior end ossifying as the articulare. The two halves of the jaw
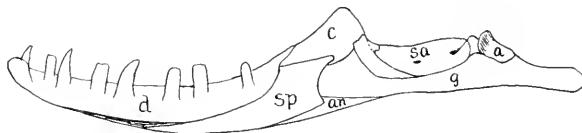
FIG. 151.—Medial side of lower jaw of *Varanus*. *a*, articulare; *an*, angulare; *c*, coronoid; *d*, dentale; *g*, goniale; *sa*, surangulare; *sp*, splenial.

are united by cartilage or suture at their anterior ends, except in Ophidia where there is a ligamentous connexion, permitting a wide distension of the mouth, and in Chelonia and Anomodonts where the halves are ankylosed. In the extreme development there are many membrane bones in the lower jaw (fig. 151). On either side of the anterior end of the Meckelian is a dentale, followed on the medial side by a splenial. At the insertion of the occludent muscles is a coronoid, and on the outer ventral side an angulare, dorsal to which is a surangulare. A goniale occurs on the medial and ventral side

of the Meckelian, usually fusing early with the articulare. The number of these bones is often reduced by fusion in the adult, sometimes by absolute loss.

The hinder of the visceral arches are reduced or absent in the adult, while the anterior branchials are more or less closely connected with the body of the hyoid. The adult Chelonia are the more primitive in retaining three independent arches (hyoid and first two branchials) the latter connected with the hyoid body. The arches may persist, in part, as cartilage, part being ossified. There are two
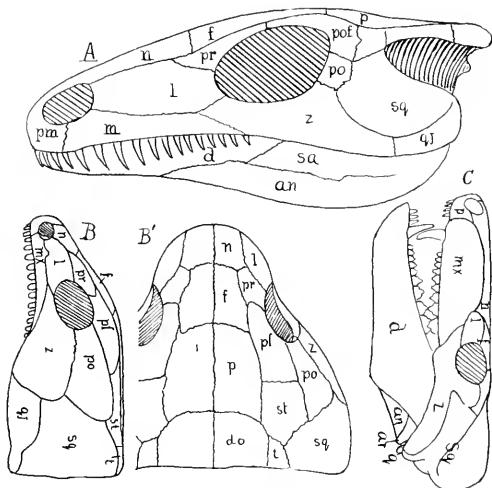
FIG. 152.—Theromorph skulls: *A*, *Seymouria* (Williston); *B*, *Pantylus* (Williston); *C*, *Cynognathus* (Gregory); *an*, angulare; *ar*, articulare; *d*, dentale; *do*, dermoccipital; *f*, frontal; *l*, lacrimal; *mx*, maxilla; *n*, nasal; *p*, parietal; *pf*, *pof*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pr*, prefrontal; *q*, quadrate; *qj*, quadratojugal; *sa*, surangulare; *sq*, squamosal; *st*, supratemporal; *t*, tabulare; *z*, zygomatic.

parts to the hyoid, cornua and body, and the relations of the former in Crocodilia support the view that a part of the ossicula auditus of reptiles (and probably of other Amniotes) has been derived from the hyomandibula (p. 119).

THEROMORPHA.—Division of reptiles into Synapsida and Diapsida (p. 138) separates the Pelycosaurs from the other forms, but for convenience all are treated here together. Only a few general statements are made here; reference must be to special papers for details. All Theromorphs have short, broad crania, usually with a parietal foramen, and beyond this opening and the orbits and nares, the roof is complete in Cotylosaurs (fig. 152), while in Therapsids there is a single temporal fossa bounded laterally by a squamoso-zygomatic arcade, which may also include the postorbital and the quadratojugal when the latter

is present. The Pelycosaurs (fig. 153) have both fossa—are diapsids. In all
the number of cranial bones is smaller than in Stegocephals. All four occipitals
are present, and usually the condyle is solely basioccipital, although occasionally
exoccipitals contribute, and in *Cynognathus*, recession of the basioccipital leaves
a pair of exoccipital condyles.

Both supratemporal and tabulare are common in the roof and rarely there
is a preparietal in front of the parietals. Parasphenoid is lacking[1] and the
pterygoids usually meet in the middle line behind the vomer. An epipterygoid
is sometimes present and the quadrate is held firmly by the squamosal. The
number of bones in the lower jaw is less than in many living species; a goniale
being rare, while coronoid and surangulare are not common. The teeth are
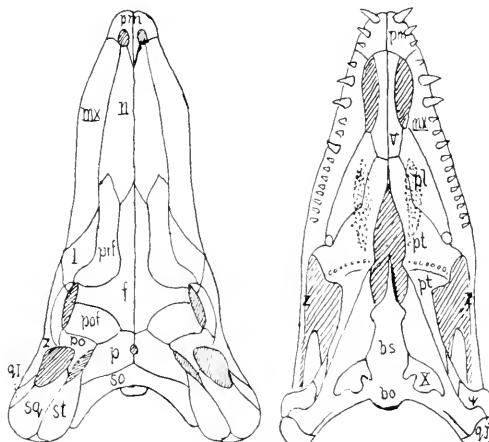
FIG. 153.—Skull of *Dimetrodon*, dorsal (Baur and Case), ventral (Broom). *bo*,
basioccipital; *bs*, basisphenoid; *f*, frontal; *l*, lacrimal; *mx*, maxilla; *n*, nasal; *p*, parietal;
pl, palatine; *pm*, premaxilla; *po*, postorbital; *pof*, postfrontal; *prf*, prefrontal; *pt*, pter-
ygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal; *st*, supratem-
poral; *v*, vomer; *x*, bone called tympanic by Broom.

thecodont (in distinct sockets) and in Theriodonts are differentiated as incisors,
canines and molars, or as in many Anomodonts there is but a pair of large upper
incisors, or teeth may be entirely lacking.

The PLACODONTIA have both Theromorph (Synapsidan) and Sauroptery-
gian relations. The temporal fossæ are large, the orbits and nares lateral. The
exoccipitals exclude the supraoccipital from the foramen magnum. The small
squamosal is united to the quadrate, and a bone, interpreted as a quadratojugal,
extends down on the lateral side of the quadrate. Pterygoid and palatines,
meeting in the middle line, are fused to support the large pavement teeth which
also occur on the maxillæ. An os transversum is present and the choanæ are far
anterior. The lower jaw has an enormous coronoid, correlated with the crush-
ing teeth of the jaws.

[1] *Pantylus* is said to have a small parasphenoid in front of the basisphenoid, but the
pertinence of this and some other genera (*e.g.*, *Seymouria*, figure 152, *A*) to the Cotylosaurs
is questionable; they appear more like Stegocephals.

CHELONIA are not closely related to any other known group, but such resemblances as they show point rather remotely to the Cotylosaurs. The skulls are compact and are characterized by a single temporal fossa, bounded by squamosal and zygomatic, a quadratojugal sometimes entering the arcade.

The chondrocranium (fig. 154) is somewhat like that of Lacertilians, but is heavier and stronger. Its parts, in the known stages, lie in one plane, there being no marked flexure between pre- and post-hypophysial parts. The arch
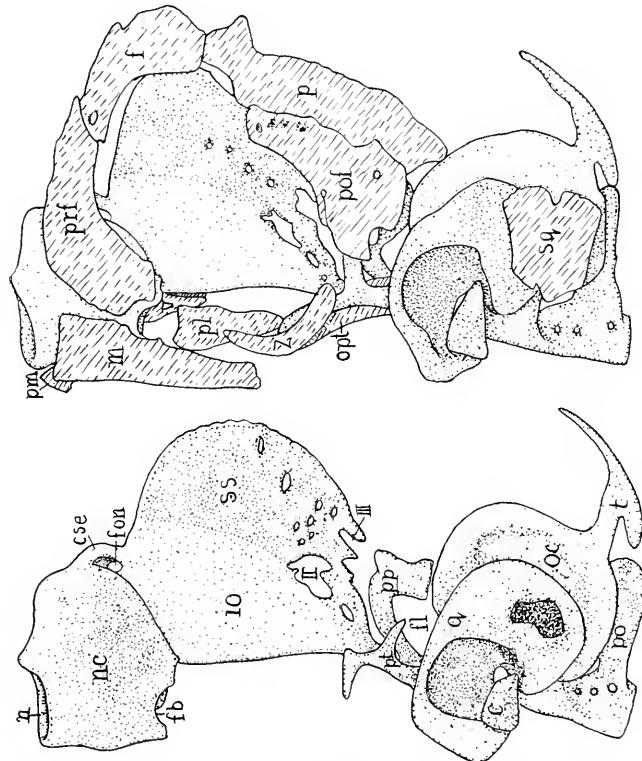
Fig. 154.—Chondrocranium of *Emys lutaria*, showing developing membrane bones (Kunkel, '12). *c*, columella; *cse*, sphenethmoid commissure; *fb*, basal fenestra; *fl*, foramen lacerum; *fon*, orbito-nasal foramen; *io*, interorbital septum; *m*, maxilla; *n*, naris; *nc*, nasal capsule; *oc*, otic capsule; *opt*, membrane pterygoid; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *po*, postotic pillar; *pof*, postfrontal; *pp*, preotic pillar; *prf*, prefrontal; *pt*, cartilage pterygoid; *q*, quadrate; *sq*, squamosal; *ss*, supraseptal plates; *t*, posterior tectum; *v*, vomer; *z*, zygomatic.

of the occipital vertebræ remains separate from the synotic tectum for some time and the metotic foramen is not closed above, while the foramen magnum is closed by a strong process from the tectum. The basal plate has a median fenestra and the plate itself narrows anteriorly to pass into the trabeculæ. Both hypophysis and internal carotids occupy the hypophysial fenestra, in front

10

of which is the common trabecula, expanded dorsally into an imperforate interorbital septum. The supraseptal plates have a regular curve and are perforated by a moderate optic foramen, behind which is a foramen for the ophthalmic artery. The prootic fissure is incomplete, no extension of the sphenolateral reaching from the preotic pillar to the otic capsule. In *Chelydra* a median parietal tænia connects the pillar with the supraseptal plate; *Emys* has none. The nasal capsules are nearly entire, the only openings being the nares, looking forwards, a fenestra olfactoria on the medial side and a basal fenestra on the posterior basal surface.

The pterygoquadrate cartilage, separate from the cranium, is divided in front into epipterygoid and pterygoid processes, while the quadrate shows the features of the adult, being expanded into a vesicle which contains part of the tympanum and is traversed by the columella. The hyobranchial skeleton is much reduced, with a rudimentary hyoid and two branchial arches, the hyoid
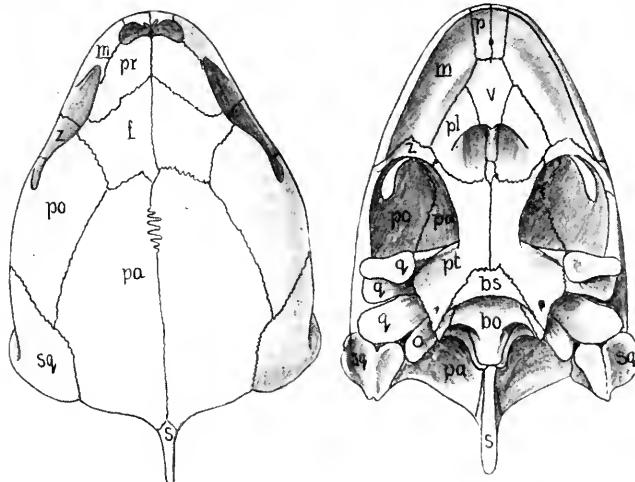
Fig. 155.—Dorsal and ventral sides of cranium of *Chelone mydas*. *bo*, basioccipital; *bs*, basisphenoid; *f*, frontal; *m*, maxilla; *o*, opisthotic; *p*, premaxilla; *pa*, parietal; *po*, postfrontal; prefrontal; *pt*, pterygoid; *q*, quadrate; *s*, supraoccipital; *sq*, squamosal; *v*, vomer; *z*, zygomatic.

copula extending back to the second branchial arch. The hyoid cornu is very short and is separate from the body in later stages, as is the first branchial arch in all known stages. In the cartilage stage the second branchial is continuous with the hyoid corpus.

The skull of adult Chelonians is compact and (especially in the marine species) suggests that of Theromorphs, although the resemblances are superficial and secondary. Among the general features are the single median naris, orbits entirely surrounded by bone, absence of supratemporal and postfrontal bones and parietal foramen. The base of the cranium has all four occipitalia, the basi-

occipital sometimes excluded from the foramen magnum. The tripartite condyle is formed by basi- and exoccipitals. In recent species the supraoccipital is prolonged backwards in a strong occipital spine, the parietals being continued along its base, these latter bones being separate and almost always (*Dermochelys* excepted) each has a vertical descending process which reaches the pterygoid, closing the cranial cavity in front. The paired frontals occasionally extend to the naris, which is otherwise bounded by premaxillæ, maxillæ and prefrontals, nasals being absent, except in *Hydromedusa* (fig. 147) and its allies. A lacrimal is absent and the premaxillæ are usually separate.

The orbit is bounded in front by maxilla and prefrontal; above (usually) by the frontal, while it is separated from the temporal fossa by zygomatic and postorbital. The temporal region shows two conditions. In marine turtles (Cryptodira, fig. 155) postorbital and squamosal extend in an arch over the origin of the muscles of the lower jaw and reach the parietal, the floor of the enclosed cavity being formed by parietal, otics, squamosal and quadrate bones (fig. 156). In other Chelonia (fig. 157) postorbital and squamosal are separate from the parietal, and pro- and opisthotic are visible from above, while the orbit is separated in some genera from the muscular pit by a bar of postorbital and zygomatic; others have no such bar, these two bones forming part of the floor of the fossa. Sometimes a quadratojugal is present between squamosal and zygomatic, sometimes it is absent.

As stated above, the cranial cavity is closed in front by the descending plates of the parietals, the alisphenoid usually not being ossified, but a few species have a bone which answers to it.

Fig. 156. — Skull of *Chelone* with roof of temporal fossa removed (Butschli, '10). *dp*, descending process of parietal; *eo*, exoccipital; *f*, frontal; *m*, maxilla; *oo*, opisthotic; *p*, parietal; *pf*, prefrontal; *pl*, palatine; *pm*, premaxilla; *po*, postfrontal; *poo*, prootic; *pt*, pterygoid; *q*, quadrate; *so*, supraoccipital; *sq*, squamosal; *z*, zygomatic.

Fibrocartilage separates the two orbits, this septum being supported by a cartilage.rostrum, the common trabecula. The septum continues forward into the nasal region.

There are one or two pairs of vacuities in the floor of the cranium (fig. 157), one lateral to the pterygoids, the second, when present, between the lateral angles of the pterygoids and the palatines. Vomers are always visible and sometimes fused in the middle line and also with the palatines. Except in *Cistudo*, *Hydromedusa*, *Trionyx*, etc., the pterygoids meet in front (fig. 155) and are articulated with the smaller basisphenoid by their medial margins, and, except in Chelonidæ, they reach the maxillæ. Where the pterygoids do not meet, the basisphenoid extends to the vomer, except in *Trionyx*
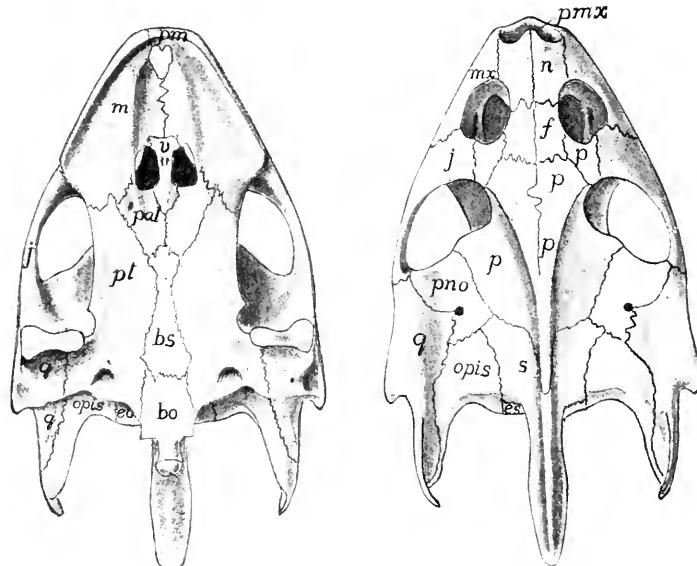
FIG. 157.—Cranium of *Trionyx*. *bo*, basioccipital; *bs*, basisphenoid; *eo*, *es*, exoccipital; *f*, frontal; *j*, zygomatic; *m*, *mx*, maxilla; *n*, prefrontal; *p*, (behind orbit) postfrontal; others parietal; *pal*, palatine; *pmx*, premaxilla; *pno*, prootic; *pt*, pterygoid; *q*, quadrate; *s*, supraoccipital; *v*, vomer.

where the palatines intervene. A distinct presphenoid occurs in *Dermochelys* and in the ontogeny of *Chelys*; but is not known in other forms. An os transversum is unknown.

The quadrate is expanded and excavate like its cartilage, and in the adult the columellar notch in its posterior border is sometimes converted into a foramen by the meeting of the margins of the gap, a condition met also in Pythonomorphs. The axis of the quadrate is nearly vertical and the bone is held immobile by squamosal and quadratojugal when the latter is present.

All of the typical bones appear in the development of the lower jaw, sometimes remaining distinct in the adult. The halves of the jaw are ankylosed in the adult. The hyoid body, perforate in *Chelys*, is more or less elongate and bears a weak entoglossal process, possibly the remnants of a hyoid-mandibular copula. The body may persist wholly as cartilage or it may ossify from one or three centres, the pair in the latter case being anterior. The hyoid cornua sometimes persist as cartilage, when ossified they are fused with
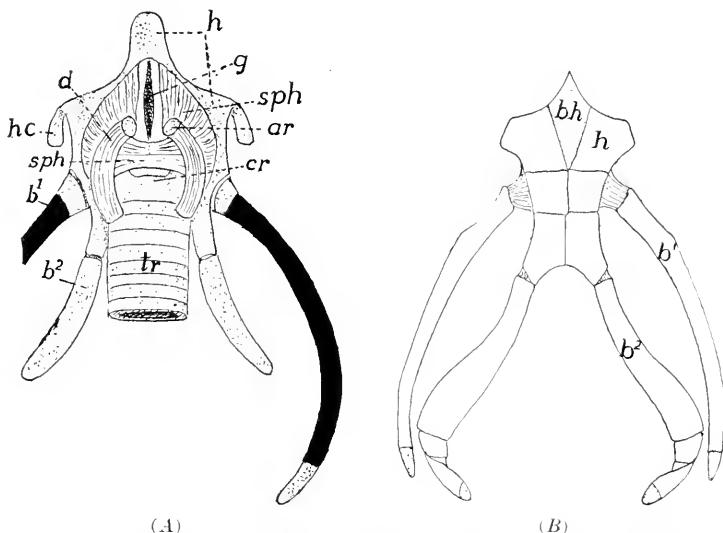
FIG. 158.—Hyoid apparatus of (*A*) *Chelone* (Göppert), and (*B*), *Trionyx*. Cartilage stippled. *ar*, arytenoid; *b*, branchial arches; *bh*, basihyoid; *d*, dilator muscles; *g*, glottis; *h*, hyoid; *hc*, hyoid cornu; *sph*, sphincter muscles; *tr*, trachea.

the body. The first branchial is ossified, at least in part, and both it and the second arch may be entire or subdivided into separate elements.

SAUROPTERYGIA have synapsidan skulls (fig. 159), with a large temporal fossa, bounded laterally by squamosal and a large bone, probably united post-frontal and postorbital, the zygomatic being excluded from the border and no quadratojugal being present, the zygomatic articulating with the squamosal. Exoccipitals sometimes form part of the occipital condyle. A parietal foramen is present between the separate parietals, each of which sends a process laterally to the squamosal, bounding the temporal fossa behind. Parietal and frontal of a side are frequently fused to a fronto-parietal, while a prefrontal excludes the frontal from the orbit. Sclerotics are absent. The orbit is close to the naris, the latter bounded by prefrontal, maxilla and premaxilla. The quadrate,

directed downwards and backwards, has no columellar notch and is covered externally for most of its length by the squamosal.

The basisphenoid is small with (usually) a small parasphenoid in front of it, lying in a pterygoid vacuity. The pterygoids are large, meet in front, and extend forwards in the middle line to the vomers, separating the palatines; behind, they articulate with the basipterygoid process of the basisphenoid. A transversum with the pterygoid and palatine, bounds a suborbital vacuity in some species, while a large subtemporal vacuity lies between pterygoid and zygomatic. The choanæ are just in front of the palatines and between vomers and maxillæ. The thecodont teeth are confined to the margins of the jaws in Plesiosaurs.
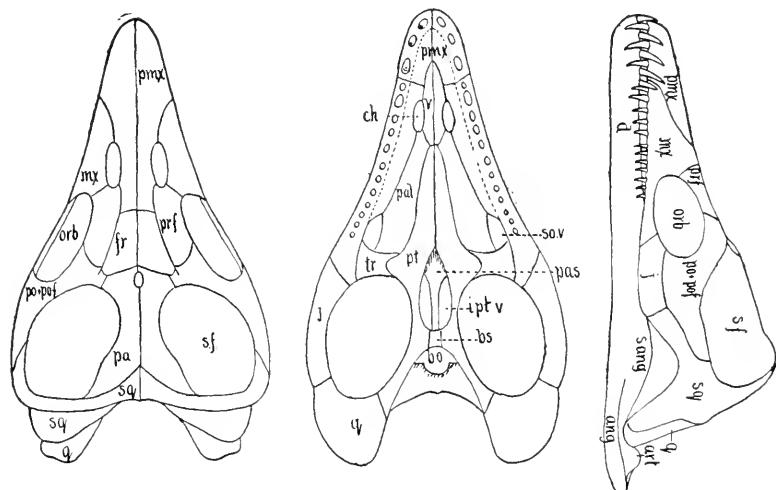
FIG. 159.—Skull of *Plesiosaurus macrocephalus* (Andrews). *an*, angulare; *ar*, articulare; *bo*, basioccipital; *bs*, basisphenoid; *ch*, choana; *d*, dentale; *fr*, frontal; *iptv*, interpterygoid vacuity; *j*, zygomatic; *mx*, maxilla; *orb*, orbit; *pa*, parietal; *pal*, palatine; *pas*, parasphenoid; *po + pof*, postorbital and postfrontal; *pmx*, premaxilla; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *sang*, surangulare; *sf*, supratemporal fossa; *sov*, suborbital vacuity; *sq*, squamosal; *tr*, transversum.

The separate bones of the lower jaw are indistinguishable as a rule, but in *Polycotylus* dentale, angulare, surangulare, goniale and articulare are recognized.

ICHTHYOSAURIA have skulls (fig. 160), evidently adapted for an aquatic life, the snout being very long and formed almost wholly of premaxillæ. The single temporal fossa, bounded laterally by supratemporal and postfrontal, has the squamosal entering but slightly or not at all into the arcade. Sclerotic bones occur in the large orbits which are close to the nares, only the lacrimal intervening. Frontals and parietals are short, the parietal foramen lying between the four bones. The short maxilla forms a small part of the upper jaw, but enters the border of the orbit. Pre- and postfrontal meet above the orbit, excluding the frontal from its margin, while the posterior and inferior borders are formed by postorbital and zygomatic.

All four occipitalia form the border of the foramen magnum and the basioccipital alone bears the condyle. Lateral to the exoccipital is an opisthotic, separate from the prootic. The quadrate is held by squamosal and quadratojugal, and joins the pterygoid on the median side. This latter bone is long; the pair, including a pterygoid vacuity between them, meet in front, separating palatines and vomers of the two sides. Behind they rest against the basisphenoid. Os transversum and epipterygoid are present. The basisphenoid is short, but prolonged forwards by a rostrum, interpreted both as a pre- and a parasphenoid. Teeth, when present, are confined to the margins of the jaw. In the lower jaw dentale, angulare, surangulare and articulare are distinct. A stout rib-like hyoid occurs, but no other traces of visceral arches are known.
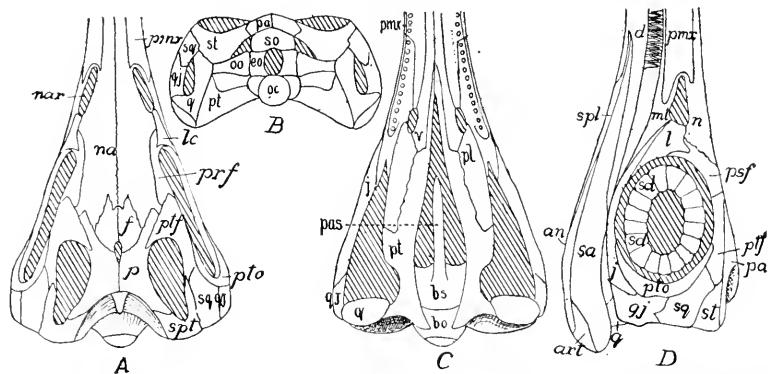
FIG. 160.—Dorsal, basal, ventral and side views of skull of *Ichthyosaurus* (Woodward, '98). *an*, angulare; *art*, articulare; *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *f*, frontal; *j*, zygomatic; *l, lc*, lacrimal; *ml*, maxilla; *n, na*, nasal; *nar*, naris; *oc*, occipital condyle; *p, pa*, parietal; *pas*, parasphenoid; *pl*, palatine; *pmx*, premaxilla; *prf, psf*, prefrontal; *pt*, pterygoid; *ptf*, postfrontal; *pto*, postorbital; *q*, quadrate; *qj*, quadratojugal; *sa*, surangulare; *scl*, sclerotics; *spl*, splenial; *st, spt*, supratemporal; *sq*, squamosal.

SQUAMATA have an elongate skull with slender bones and, except in a few lizards, a moveable quadrate, which lies in front of the tympanic cavity. The lower temporal arcade is never complete, and in most genera (snakes and some lizards excepted) the upper arcade is formed by postfrontal and squamosal. Another squamosal process (absent in Ophidia) may meet the parietal, limiting the large posttemporal fossa. A parietal foramen is present, except in Ophidia, and usually parietals, frontals and premaxillæ of the two sides are fused in the middle line. The nares are separate. Palatal processes of maxillæ and premaxillæ are weakly developed. The paired vomers are always visible and the palatines may or may not meet in the middle line. The pterygoid vacuity is large, the pterygoids extending back to the quadrate and also articulating with a more or

less pronounced basipterygoid process of the basisphenoid. Except
in Amphisbænans and *Chameleo* (fig. 165) epipterygoid and trans-
versum are present. The basisphenoid is continued forwards by
a longer or shorter rostrum, apparently parasphenoidal. The bones
in the lower jaw are numerous except in Ophidia where there is some
fusion.

The chondrocranium is best known in lizards. In the early stages (fig. 161)
only parachordals, trabeculæ and sphenolateral parts are present in front and
there are four incomplete arches in the postotic regions, these separating the
roots of the twelfth nerve—the same number as in Mammals and three more
than in Amphibia. The basal plate is completed later (fig. 162), the parachor-
dals meeting ventral to the chorda, the posterior part of each side arising as
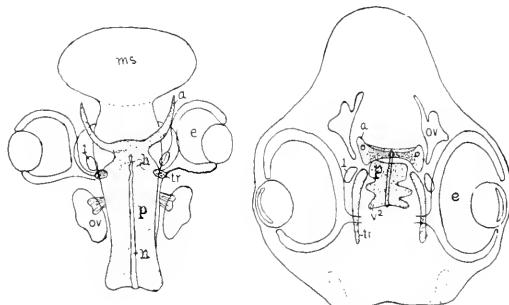
FIG. 161.—Reconstruction of chondrocranium of *Ascalabotes* (Sewertzoff, '00).
a, sphenolateral; *e*, eye; *h*, hypophysis; *ms*, mesencephalon; *ov*, otic vesicle; *n*, notochord;
p, parachordal plate; *tr*, trabecula; *v*, second occipital vertebra; 1, first head somite.

a pillar (vertebral arch) with the ninth nerve between it and the otic capsule,
the tenth and eleventh nerves behind it. The posterior edge of the basal plate
is excavate, separating a pair of occipital condyles, the excavation disappearing
later, resulting in the single condyle of the adult. Chondrification of each otic
capsule begins in the floor, the median wall being last to develop, while, to
accommodate the large lagena, the epithelial parts of the ear invade the basal
plate. The connexion of the two capsules by the synotic tectum is later. The
tectum, arising from both capsules and occipital vertebræ, bears a median
anterior process as in Anura.

At first each trabecula is a separate bar at a strong angle with the posterior
part of the cranium. Later the two extend forwards and fuse as the trabecula
communis, uniting behind with the basal plate. The common trabecula expands
dorsally as the interorbital septum, dividing dorsally into the supraseptal plates,
each usually with a septal fenestra. Each trabecula gives off laterally behind,
a basipterygoid process, apparently arising from pterygoid tissue, the rest of
which forms the pterygoquadrate.

The relations of the sphenolateral parts to later conditions are uncertain.
In *Lacerta* (fig. 144) there is a marginal tænia which joins the roof of the otic

capsule to the supraseptal wall, and ventral to this is a medial parietal tænia, also extending from the supraseptal plate to the prootic pillar, bounding the metoptic fenestra above. These two tæniæ are joined by a vertical bar which extends down to the common trabecula. In *Eumeces* only the part of this bar below the medial tænia is present. Apparently both tæniæ and the vertical bar are the homologues of the Elasmobranch sphenolateral.
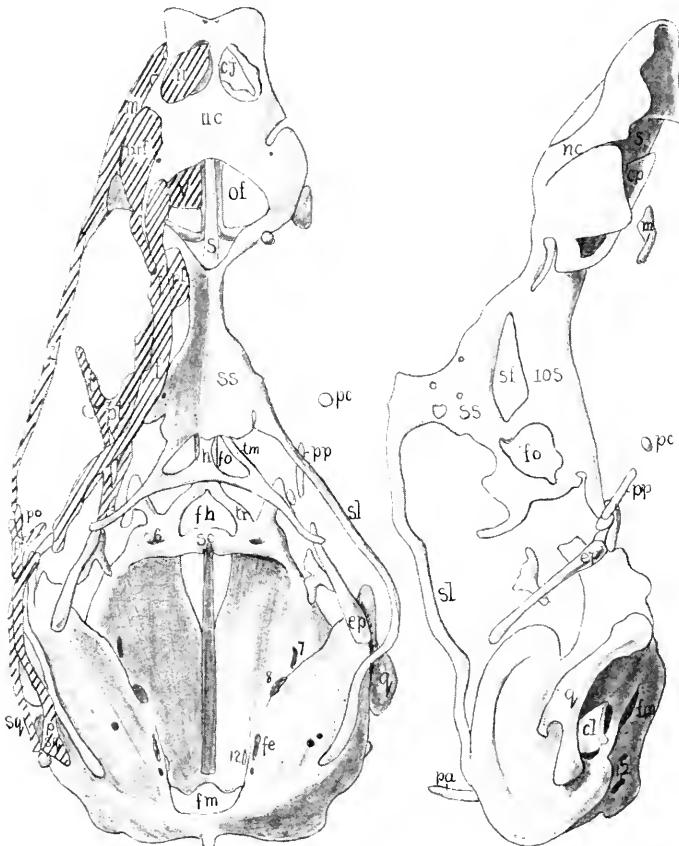
FIG. 162.—Chondrocranium and early membrane bones of *Eumeces 5-lineatus* (Rice, '20). *cl*, columella; *cp*, paraseptal cartilage; *ep*, epipterygoid; *f*, frontal; *fe*, endolymph foramen; *fh*, fenestra hypophyseos; *fm*, foramen magnum; *fo*, optic foramen; *h*, hypochiasmatic bar; *ios*, interorbital septum; *m*, maxillary cartilage; *n*, nasal; *of*, olfactory foramen; *p*, parietal; *pa*, ascending process; *pc*, anterior pterygoid cartilage; *pf*, postfrontal; *pl*, palatine; *po*, postorbital; *pp*, posterior pterygoid cartilage; *prf*, prefrontal; *pt*, pterygoid bone; *q*, quadrate; *s*, nasal septum; *sc*, sellar crest; *sf*, septal fenestra; *sl*, sphenolateral; *sq*, squamosal; *ss*, supraseptals; *t*, transversum; *tr*, trabecula; *v*, vomer; *z*, zygomatic.

The upper margin of the supraseptal plate is connected with the nasal capsule by a slender sphenethemoid bar. The capsule has a strong internal process

(concha) to support the olfactory membrane, and in the floor is a paraseptal cartilage, parallel to the nasal septum, which lies below the vomero-nasal organ. The pterygoquadrate consists of a pterygoid part and an epipterygoid process, the quadrate chondrifying separately, there rarely being a connexion between the two. Meckel's cartilage has a strong retroarticular part projecting behind the articulation of the jaws. The hyobranchial apparatus consists of hyoid and two branchial arches. The hyoid furnishes the columellar structures which arise as a continuum and later form two cartilages, the **oto-** and **hyostapes** of Hoffmann. Then the otostapes divides, the part adjoining the vestibular fenestra forming the adult stapes, the rest and the hyostapes giving rise to the columella. The branchial arches join the hyoid body, and vary greatly in detail in different genera. The homology of the entoglossal process is uncertain.

LACERTILIA.—The lizard skull is primitive in some respects. No farther reference to the chondrocranium is necessary save to say that a considerable part of the cartilage persists through life, more in

FIG. 163.—Base of cranium of *Varanus. bo,* basioccipital; *bs,* basisphenoid; *eo,* exoccipital; *pa,* parietal; *po,* postorbital; *pt,* pterygoid; *q,* quadrate; *s,* squamosal; *so,* supraoccipital.

chameleons than in others. Some lizards have incomplete ossification of the parietals, leaving fontanelles in the roof (*Stellio, Sceloporus,* etc.). The alisphenoid never ossifies, and in the adult fused bones, sometimes of diverse origin, are common. The cartilage bones are mostly in the occipital and otic regions, with some in the orbital. All four occipitalia are present (fig. 163), the supraoccipital frequently extending over the otic capsule; the occipital condyle is entirely basioccipital. Pro- and opisthotic arise separately, the latter fusing early with the exoccipital to an **otoccipital bone,** the opisthotic furnishing the parotic process, which sometimes extends laterally to articulate with the quadrate. The basisphenoid has a well-marked sellar crest on its anterior internal margin, while the parasphenoid fuses early with the bone. The cartilage bar of the orbital region develops the orbitosphenoid, and in old individuals occipitals and sphenoid fuse to a basal bone. There is little ossification of the interorbital septum.

The membrane bones are numerous at first, including parietals, frontals, nasals, premaxillæ, maxillæ, pre- and postfrontals, zygomatics, lacrimals and squamosals on the dorsal surface; on the ventral

are vomers, palatines, pterygoids, transverse and parasphenoid, with a septomaxillary in the nasal capsule, resting on the nasal septum and lateral wall of the labyrinth; it is apparently the same as the bone in Amphibia, but is deeper in the capsule. Parietals and frontals are fused in pairs, except in some of the more aberrant genera. When the parietals form the whole of the roof of the cranial cavity, the parietal foramen is between them, but when the frontals enter the roof, the foramen is between the four bones. Occasionally, as in *Anniella*, the foramen is lacking. The premaxillæ are fused and send
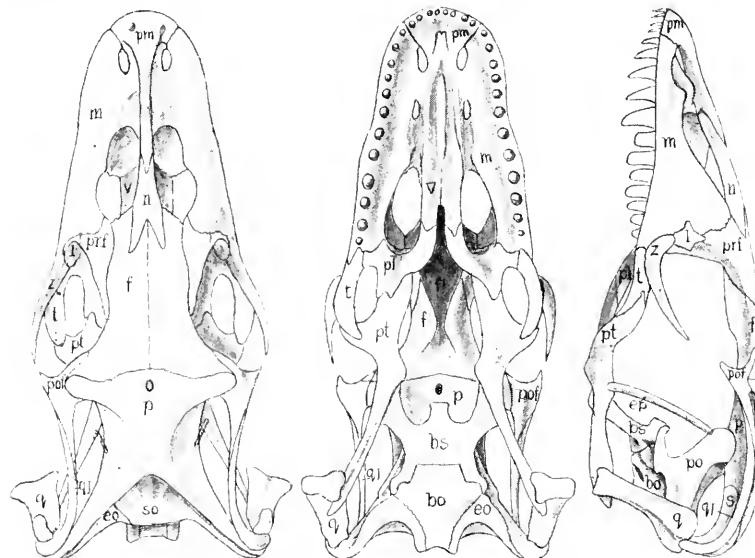
FIG. 164.—Cranium of *Varanus*. *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *ep*, epipterygoid; *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *po*, prootic; *pof*, postfrontal; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal; *t*, transversum; *v*, vomer; *z*, zygomatic.

a process back to the nasals. As in most Squamata, there is a single postfrontal-squamosal arcade (zygomatic also in *Chameleo*, figure 165) bounding the temporal fossa laterally while a postorbital arcade of zygomatic and postorbital separates orbit and temporal fossa, but is more or less reduced in *Varanus*, *Gecko*, etc.

The most constant vacuities in the cranial floor are one lateral to each vomer, and another medial, bounded by palatines and pterygoids. Pterygoid and basisphenoid have a basipterygoid articulation. The parasphenoid is paired in origin in *Lacerta*, the

halves uniting later and giving off an anterior rostrum which closes
the hypophysial fenestra.   The squamosal is long and slender and
is moveably articulated with the quadrate.   None have a quadrato-
jugal and the zygomatic is lacking in Amphisbænans.

   The lower jaw has the normal six bones (fig. 151), distinct in the
young and persisting so in many genera, except that the goniale
fuses with the articulare.   The teeth in both jaws are either acrodont
or pleurodont, and teeth also occur on the palatines except in aber-
rant genera.   The hyoid apparatus varies; it always has a small
body, and supports two pairs of cornua and a well developed ento-
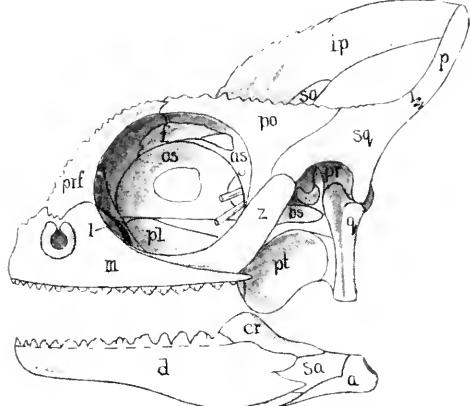
Fig. 165.   Fig. 166.

FIG. 165.—Side view of skull of *Chameleo* (Parker, '80).   *a*, articulare; *as*, alisphe-
noid; *bs*, basisphenoid; *cr*, coronoid; *d*, dentale; *f*, frontal; *ip*, interparietal; *l*, lacrimal
m, maxilla; *os*, orbital septum; *p*, parietal; *po*, postorbital; *prf*, prefrontal; *pt*, pterygoid
q, quadrate; *sa*, surangulare; *so*, supraoccipital; *sq*, squamosal; *z*, zygomatic.
   FIG. 166.—*A*, Hyoid apparatus of *Heloderma*.   *b*, branchial cornu; *c*, hyoid copula
h, hyoid cornu.
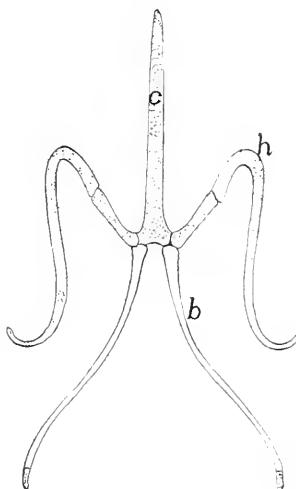
glossal process.   The upper end of the adult hyoid has lost its con-
nexion with the columella and has moved backwards, and in Geckos
is connected with the otoccipital by a cartilage of uncertain
homology.   The branchial arches, usually long, consist of one or two
articles, the halves of the second arch is some genera lying close
together and extending far backwards.

   PYTHONOMORPHA.—These aquatic lizards of former days differ less from true
lizards in skull (fig. 167) than in other parts of the skeleton.   Parietals, frontals

and premaxillæ are fused in the same way and the nasals are united to the premaxillæ. They have a parietal foramen. The exoccipitals have strong parotic processes, possibly otoccipital. Vomers and palatines of the two sides are distinct, but the latter touch in the middle line. The mobile quadrate, articulated dorsally to the squamosal, is either notched or perforate for the columella, recalling the Chelonia. The orbit (containing sclerotic bones) is closed behind by an arcade formed by zygomatic and (apparently) fused post-orbital and postfrontal bones, a posterior process of which meets the squamosal to form the temporal arcade. The transversum is small and connects only
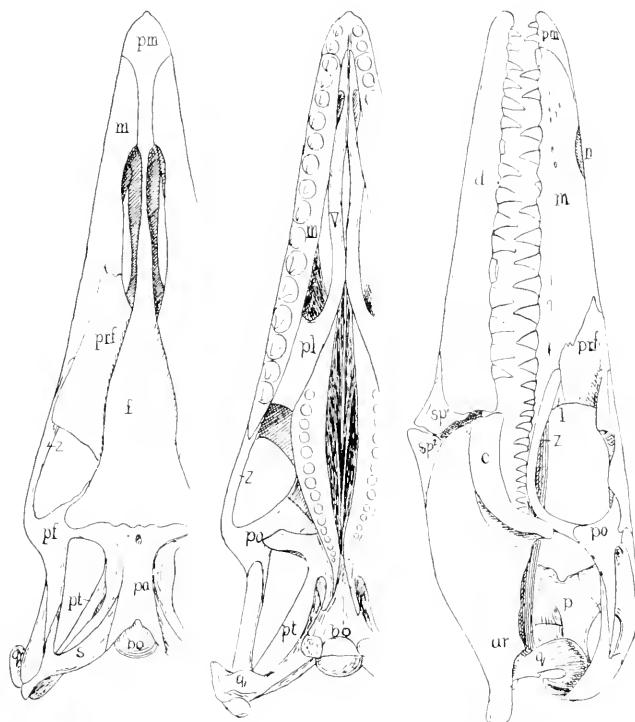
FIG. 167.—Dorsal, ventral and side views of skull of *Clidastes velox* (Williston, '98). *ar*, articulare; *bo*, basioccipital; *c*, coronoid; *d*, dentale; *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, naris; *p*, petrosal; *pa*, parietal; *pf*, postfrontal; *pl*, palatine; *pm*, premaxilla; *po*, postfrontal; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *sp*, splenial; *sq*, squamosal; *v*, vomer; *z*, zygomatic.

pterygoid and zygomatic, the latter extending so far forwards as to exclude the maxilla. There are fewer bones in the lower jaw than in embryo lizards and a peculiarity is that between dentary and splenial in front, and coronoid, angulare and surangulare behind, there is a hinge which permitted a wide separation of the anterior parts of the jaw, this freedom apparently being increased by a ligament, as in snakes, between the tips of the two halves of the jaw.

OPHIDIA.—The snake skull is somewhat reduced, but still shows plainly Squamate characters, though lacking a parietal foramen. The history of the chondrocranium is largely unknown, all studies of it having been made before the introduction of modern methods. A brief statement of the little known follows:

In the early stage (fig. 168) the notochord nearly reaches the hypophysis, later its anterior end disappears, its tip now lying between the otic capsules, while the basal plate, with a basicranial fenestra, is united to the otic capsules, and the metotic pillar is connected dorsally with the capsule which is larger than in most lizards. Its medial and lateral walls chondrify late, the ninth nerve passing through the median wall together with the perilymph duct. The trabeculæ, separate for most of their length, are close together in front of the hypophysis, and their anterior ends lie in front of the cerebrum and give rise to a low interorbital septum, which supports dorsally a pair of supraseptal plates, which, unlike the septum, chondrify. The rest of the history has not been followed. The nasal capsule is formed by nasal septum, trabecular cornu and a dorsal enclosing plate. The visceral skeleton consists of mandibular and hyoid arches, no branchials having been seen. The pterygoid is simple and lacks processes. The columella arises from the upper end of the hyoid, the rest of the arch separating and wandering farther back.

FIG. 168.—Chondrocranium of *Tropidonotus* (Parker, '79). *ac*, anterior semicircular canal; *c*, carotid canal; *fb*, basicranial fenestra; *fh*, hypophysial fenestra; *lc*, lateral canal; *nc*, nasal capsule; *pc*, posterior canal; *st*, synotic tectum.

The adult skull, which is well ossified, has fewer bones than other Squamates, the result of both fusion and failure to develop. The cranial cavity (fig. 169), extending to the orbital region, is closed in front by downgrowths from frontals and parietals which meet well ossified ali- and orbitosphenoids. The small premaxillaries bear teeth only in the larger serpents. The maxillæ are moderate and, except in poisonous species, bear numerous teeth. In venomous species the maxilla is reduced to a base for the single poison fang, and is so hinged that it folds back on the roof of the mouth when the mouth is closed, and erects when the mouth is opened. The mechanism involved in this includes quadrate, pterygoid and transversum, which slide forwards, turning the maxilla on its hinge (fig. 170). Zygomatic and quadratojugal bones are lost as are both temporal

arches, except in so far as the upper is represented by the elongate squamosal and its ligamentary attachment to the parietal bone;
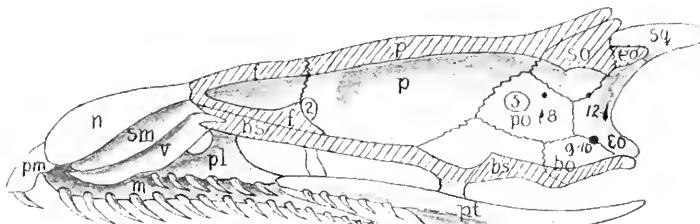
FIG. 169.—Section of skull of *Python* (Bütschli, '10). *bo*, basioccipital; *bs*, basi-sphenoid; *eo*, exoccipital; *f*, frontal; *m*, maxilla; *n*, nasal; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *po*, prootic; *pt*, pterygoid; *sm*, septomaxillary; *so*, supraoccipital; *sq*, squa-mosal; *v*, vomer.

its lower end is loosely connected with the upper end of the quadrate. The postfrontal bone is usually well developed; *Typhlops* has lost the squamosal.

Pterygoids and frequently the pala-tines bear acrodont teeth and are loosely connected with the cranium, and those of the two sides are remote from each other. The pterygoids are long and slender, articulating behind with basi-sphenoid and quadrate, and connected laterally with the maxilla by the trans-versum. An epipterygoid is lacking and the palatines do not articulate with cranium or vomer. The exoccipitals, which have a weak parotic process, exclude the supraoccipital from the foramen magnum; basisphenoid and basioccipital are not fused, and the former is either broad in front (some poisonous species) or is continued for-wards by a slender rostrum.

The quadrate, articulated dorsally with the squamosal and never with the

FIG. 170.—Diagram of skull of Solenoglyph snake with open and closed jaws (Bütschli, '10). *m*, maxilla; *md*, mandible; *p*, poison tooth; *pf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *s*, squamosal; *t*, transversum.

parotic process, is very mobile and aids in the protrusion and retraction of the lower jaw; its part in the erection of the fang was mentioned above. The bones of the lower jaw are more exten-

sively fused than in other Squamata, there being but four separate bones in adult rattlesnakes and some other poisonous species, and five at most in other forms. The halves of the lower jaw are connected in front by an elastic ligament, permitting a wider opening of the mouth. The hyoid is represented by a curved cartilage bar or is absent.
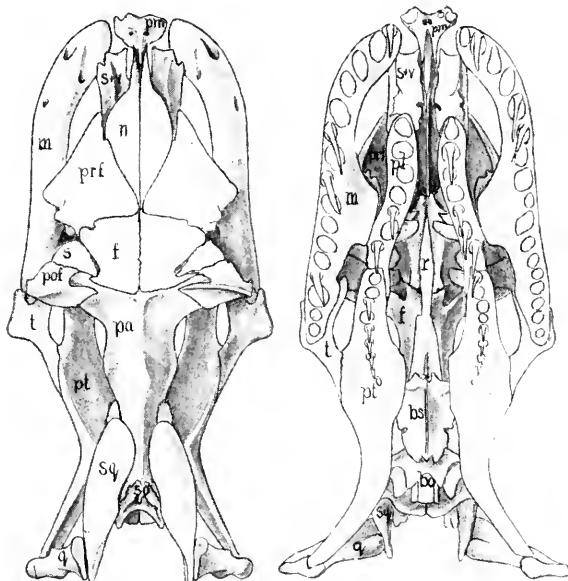
FIG. 171.—Cranium of *Python reticulatus*. *bo*, basioccipital; *bs*, basisphenoid; *f*, frontal; *m*, maxilla; *n*, nasal; *pa*, parietal; *pl*, palatine; *pm*, premaxilla; *pof*, *prf*, post- and prefrontals; *pt*, pterygoid; *q*, quadrate; *r*, rostrum; *s*, supraorbital; *so*, supraoccipital; *sq*, squamosal; *s + v*, septomaxillary and vomer; *t*,transversum.

RHYNCHOCEPHALIA.—This group, represented today only by *Sphenodon*, is related to the Lacertilia, the chief distinctions being, so far as skull is concerned, a fixed quadrate and the presence of all three temporal fossæ.

These lacertan resemblances exist in the chondrocranium, but the cartilages are more extensive and the prechordal part arises separately from, and at an angle to the posterior portion (fig. 172), the flexure being lost later. The basal plate is entire and is connected with the otic capsules, the medial walls of which long remain open. The sphenolateral cartilage is connected with the basal, and the interorbital septum supports supraseptal plates.

At a later stage the synotic tectum, formed entirely by growth from the otic capsules, sends a bar forwards which surrounds the parietal eye. The spheno-lateral becomes connected with the supraseptal by marginal and lateral teniæ,

the former bounding dorsally a large epioptic fenestra, and a metoptic fenestra arises by the coalescence of the foramina for nerves III and IV, distinct in earlier stages. The prootic pillar is connected by a bar with the otic capsule above the fifth nerve. A paraseptal cartilage connects the supraseptal plate with the nasal capsule which has a single concha.

The mandibular arch arises as a continuum, its upper part being largely quadrate with pterygoid and epipterygoid processes (fig. 172). The hyoid
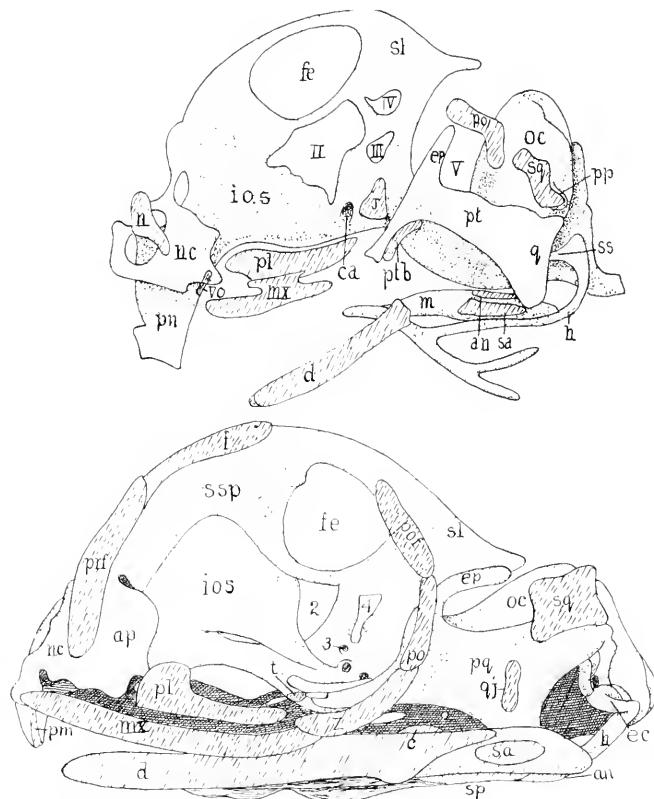
FIG. 172.—Chondrocranium and early bones of *Sphenodon;* upper figure (Howes and Swinnerton, '01) earlier; lower (Gaupp, '05) a little later; cartilage stippled, bones lined; *an,* angulare; *ap,* antorbital plate; *c,* coronoid; *ca,* carotid foramen; *d,* dentale; *ec,* extracolumella; *ep,* epipterygoid; *f,* frontal; *fe,* epioptic fenestra; *h,* hyale; *ios,* interorbital septum; *j,* zygomatic; *mx,* maxilla; *n,* nasal; *nc,* nasal capsule; *oc,* otic capsule; *pl,* palatine; *po,* postorbital; *pof,* postfrontal; *pp,* parotic process; *pq,* pterygoquadrate; *pt,* pterygoid cartilage; *ptb,* pterygoid bone; *q,* quadrate; *qj,* quadratojugal; *sa,* surangulare; *sl,* sphenolateral; *sp,* splenial; *sq,* squamosal; *ssp,* supraseptal plate; *ss,* suprastapedial; *t,* transversum; *v,* vomer; *z,* zygomatic; II–V, 2–4, nerve exits.

arch at first is in continuity with the stapes, its basal part later forming the extracolumella. The lower parts of the hyoid of the two sides are connected

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by a continuous copula with the two reduced branchial arches, the first of which becomes the posterior cornu of the adult.

The adult skull (fig. 173) has three temporal fossæ, the lower arcade consisting of squamosal, quadratojugal and zygomatic, the upper of postorbital and squamosal, while an arcade, a process of the squamosal which extends to the parietal, separates the superior fossa from the posterior. The large orbit is bounded by prefrontal, maxilla, zygomatic, postorbital, postfrontal and frontal, there being no lacrimal. The parietal foramen is between the narrow parietals which form nearly the whole of the roof of the brain case. The
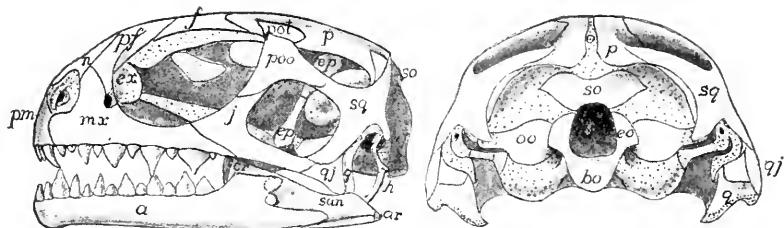
FIG. 173.—Side and basal views of cranium of young *Sphenodon* (Howes and Swinnerton, '01). Cartilage stippled. *a*, dentale; *ar*, articulare; *bo*, basioccipital; *cr*, coronoid; *eo*, exoccipital; *ep*, epipterygoid; *ex*, extranasal; *f*, frontal; *h*, hyoid; *j*, zygomatic; *mx*, maxilla; *n*, nasal; *oo*, opisthotic; *p*, parietal; *pf*, prefrontal; *pm*, premaxilla; *pof*, postfrontal; *poo*, postorbital; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal.

separate nares are almost terminal. The pterygoids (fig. 174), which have a basipterygoid articulation with the basisphenoid, extend forwards to the vomers and separate the palatines of the two sides. A transversum is present and the epipterygoid extends to the parietal. Both squamosal and quadratojugal fix the quadrate, the quadratojugal being forced ventrally by the long posterior process of the zygomatic which connects with the squamosal. Dentale, splenial, coronoid, angulare and surangulare are separate in the adult. The hyoid apparatus has a body and two pairs of cornua, the anterior (hyoid) persisting as cartilage connected with the stapes through life. The posterior cornua are ossified except at the tips.

A number of fossil genera, once included in the Rhynchocephala, have been transferred to other orders, but, as little is known of the skulls of these, they may be grouped here. All are diapsidan, so far as known, the fossæ being large in *Palæohatteria* (fig. 175) and *Champosaurus*, the latter genus, like *Sauranodon* and *Rhynchosaurus*, lacking a parietal foramen; it also had a snout elongate as in Gavials. *Procolophon* (fig. 78), which is near the ancestors of the Rhynchoce-

phals and to the Cotylosaurs, has but the lower fossa, while the wide separation of postorbital and postfrontal suggest that the upper fossa is merged with the orbit. This genus has a large parietal foramen, an epipterygoid and a vacuity lateral to either pterygoid, and an interpterygoid space. Sclerotics are present, while the posterior lateral angle of the cranium is formed by a so-called epiotic (tabulare).

The THALATTOSAURIA are extinct aquatic reptiles with Rhynchocephalian affinities. The infratemporal fossa is the larger, the two being separated by postfrontal and squamosal, the lower arcade consisting of zygomatic and possibly squamosal, a quadratojugal being absent. The naris, near the orbit, is bounded by frontal, nasal, maxilla and premaxilla, the latter bone being long. Parietals and frontals are paired; pre- and postfrontal meet above the orbit, the rest
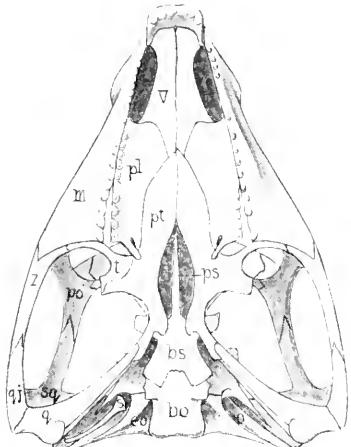
FIG. 174.   FIG. 175.

FIG. 174.—Palatal surface of Sphenodon (McGregor, '06). *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *m*, maxilla; *o*, opisthotic; *pl*, palatine; *po*, postorbital; *ps*, presphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *s*, stapes; *v*, vomer; *z*, zygomatic.

FIG. 175.—Skull of *Palæohatteria* (Jaekel, '11). *a*, articulare; *an*, angulare; *c*, coronoid; *d*, dentale; *f*, frontal; *l*, lacrimal; *m*, maxilla; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *prf*, prefrontal; *qj*, quadratojugal; *s*, splenial; *su*, surangulare; *sq*, squamosal; *z*, zygomatic.
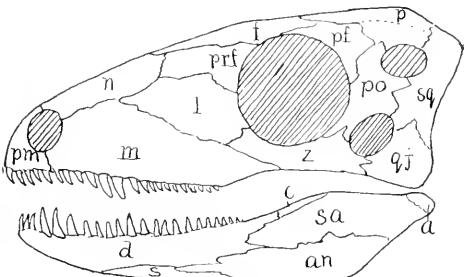
of its border being formed by lacrimal and zygomatic, no postorbital occurring. Sclerotics are present. The choanæ, just ventral to the nares, are bounded by maxillæ and palatines, and it is uncertain whether the toothed vomer is single or paired. What are called pterygoids are toothed, and apparently an epipterygoid occurs. The long dentale is largely on the medial side of the lower jaw, the angulare extending far forwards on the outer side. The articulare also is long, its anterior end being covered by a large splenial; the coronoid strong and the surangular large.

CROCODILIA.—The chondrocranium (fig. 176) is more like that of lizards than that of any other group. It lacks a basicranial fenestra, the posterior tectum is nearly vertical, not horizontal as in lizards. The basipterygoid processes are reduced, while the basitrabecular processes are large, as in birds.

The prootic pillar is well developed, a bar connecting it with the otic capsule. In front it is connected with the supraseptals by marginal and medial parietal tæniæ, which have no connecting cross bar. The interorbital septum is imperforate and sphenethmoid cartilage and orbitonasal fenestræ are lacking. The columella auris is connected with the hyoid (ceratohyoid), and the ventral part of the arch forms the small anterior cornu.
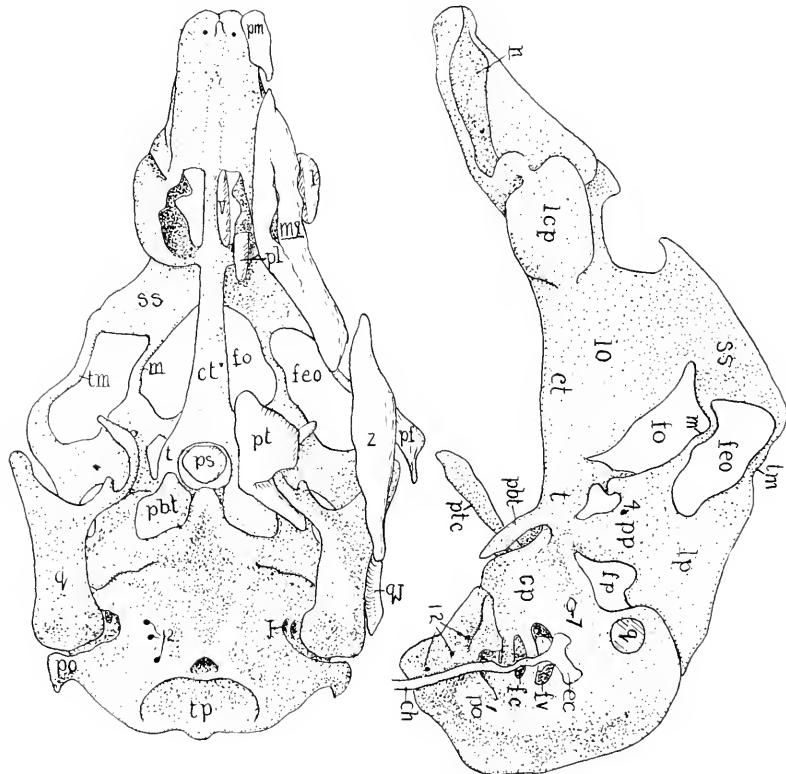
FIG. 176.—Side and ventral views of chondrocranium of *Crocodilus* with membrane bones of left side of latter (Shiino, '14). *ch.* ceratohyoid; *cp*, cochlear prominence; *ct.* trabecula communis; *ec*, extracolumella; *fc, feo*, cochlear and epioptic fenestræ; *fo, fp.* optic and prootic fenestræ; *fv*, vestibular fenestra; *io*, interorbital septum; *j*, jugular foramen; *l*, lacrimal bone; *lcp*, posterolateral concha (anterior, just in front of it); *lp*, parietal lamina; *m*, median lateral tænia; *mx*, maxilla; *n*, naris; *pbt*, basitrabecular process; *pf.* postfrontal; *pl*, palatine; *pm*, premaxilla; *po.* parotic crest; *pp*, preotic pillar; *ps.* parasphenoid; *pt.* pterygoid bone; *ptc*, pterygoid cartilage; *q*, quadrate; *qj.* quadratojugal; *ss*, supraseptal plate; *t*, trabecula; *tm*, marginal tænia; *tp*, posterior tectum; *v*, vomer; *z*, zygomatic.

The skull of the adult Crocodilia (figs. 177, 178) is elongate, has both superior and inferior fossæ, and in recent species the posttemporal fossa is open. The superior fossa is small, the inferior larger in earlier than in recent species. All occipitalia are distinct,

except that the exoccipital is fused with the opisthotic, forming a strong parotic process. Parietals and frontals are short and there is no parietal foramen. The orbits are far posterior, the nares nearly terminal, and confluent in some species. The orbits are closed behind by a process from the zygomatic to the postfrontal. The older fossils have an antorbital vacuity bounded by maxilla and nasal, but this is united with the orbit in recent genera. The zygomatic arch is complete, the zygomatic bone reaching the quadratojugal.

The cranial floor varies. All have the choanæ posterior to the primitive position, the older groups having a palate formed by the
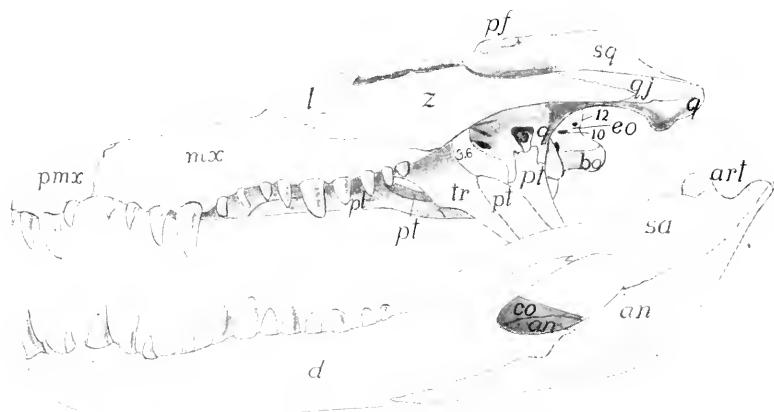
FIG. 177.—Skull of *Caiman latirostris* (Reynolds, '97). *an*, angulare; *art*, articulare; *co*, coronoid; *d*, dentale; *eo*, exoccipital; *l*, lacrimal; *mx*, maxillary; *pf*, postfrontal; *pl*, palatine; *pmx*, premaxilla; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sa*, surangulare; *sq*, squamosal; *tr*, transversum; *z*, zygomatic.

palatal processes of maxillæ and premaxillæ, the choanæ at its hinder margin, separated by the postero-lateral parts of the vomers. In *Telosaurus*, etc. the palatines meet, carrying the choanæ farther back. The next step is the covering of the vomers (*Goniopholis*, etc.) by the palatines and the meeting of the anterior ends of the pterygoids. In existing genera the pterygoids have met so far back that the vomers and the anterior end of the basisphenoid are covered, and the choanæ are near the posterior end of the cranium (fig. 178), the vomers now being thin plates between the nasal passages. In older Crocodilia the Eustachian tube lies in a groove on the ventral side of the basisphenoid; in recent species, the grooves of the two sides close to tubes with a common opening behind the posterior end of the

basisphenoid. Recent species have a large transversum, (lacking in some extinct species) in front of which is a large palatal vacuity. Pterygoid and transversum give off a strong ventral process on which the mandible plays.

A distinct alisphenoid on either side closes the cranial cavity in front; an orbitosphenoid is lacking. The large interorbital septum (cartilage or partially ossified) is supported on the cartilage rostrum and continues as the nasal septum. The quadrate is fixed on the upper medial surface by the squamosal, by the quadratojugal on the antero-inferior side. The quadrate extends obliquely backwards and downwards, so that the tympanic cavity lies above it. Teeth are confined to the margins of the jaws and are thecodont in all families. All of the bones of the lower jaw, goniale excepted, retain their individuality, and there is a large vacuity on both lateral and medial sides (fig. 177), and in some genera the articulare is perforated by a tube (**siphoneum**) leading to the interior of the bone, and containing an air passage coming from the quadrate. The large, nearly quadrate, hyoid body is cartilage (sometimes partly ossified) and is concave above to accommodate the larynx. It bears a pair of ossified cornua, regarded as the first branchial arch; the cornua are not connected with the cranium.

FIG. 178.—Floor of skull of *Alligator*. *bo*, basioccipital and condyle; *c*, choanæ; *e*, opening of Eustachian tube; *m*, maxilla; *pl*, palatine; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *z*, zygomatic.

PARASUCHIA (Phytosauria) (fig. 179) are related in skull structure to Rhynchocephals, Crocodiles and Dinosaurs. The separate nares are far back on the cranium and have vacuities beside them. Both temporal fossæ occur, separated by an arcade largely postorbital, the squamosal contributing but little. Parietals and frontals are paired and some have a parietal foramen. The choanæ are just behind the palatal processes of the maxillæ, palatines and pterygoids not meeting in the middle line. Apparently Meckel's cartilage was largely persistent, and there is a vacuity on the outer side of the lower jaw. The animals were like crocodiles in form and general relations of cranial bones; like Rhynchocephals in having postorbitals, paired frontals and parietals, and
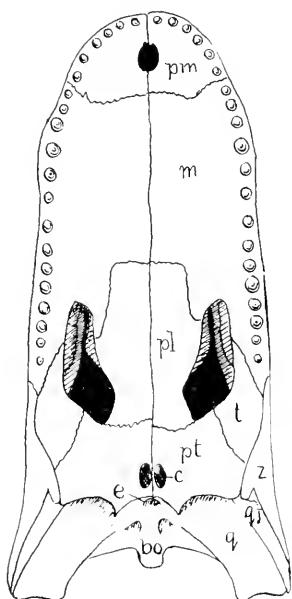
choanæ separated by the vomers. The more posterior nares, large antorbital vacuities, a short basisphenoid, and the approach of the pterygoids to the middle line suggest Dinosaurs.

PTEROSAURIA.—The skulls (fig. 180) of these extinct flying reptiles are decidedly bird-like in shape, in the angle at which they are borne on the vertebral column, and the extent to which sutures are obliterated. The lack of teeth in
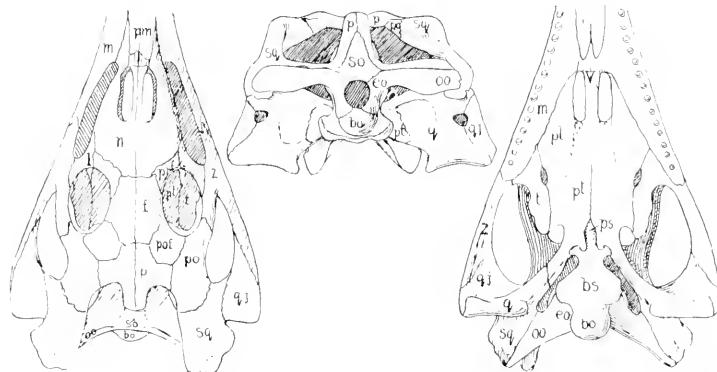
FIG. 179.—Dorsal, ventral and basal views of hinder part of cranium of *Mystriosuchus* (McGregor, '06). *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *oo*, opisthotic; *p*, parietal; *pl*, palatine; *po*, postorbital; *pof*, postfrontal; *prf*, prefrontal; *pa*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal; *t*, transversum; *z*, zygomatic.

the elongate beak of some species increase the resemblance; but there are many differences. Both temporal fossæ are present, the lower a narrow cleft behind the orbit, the quadrate forming its posterior wall. The superior fossa is far back on the cranium. The base of the skull looks obliquely down and back, and the skull is nearly at right angles with the neck. There is no parietal
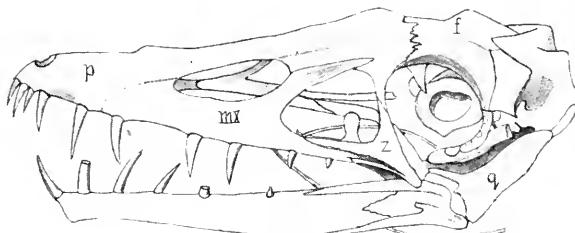
FIG. 180.—Skull of pterodactyl (*Scaphognathus*, Zittel, '90). *f*, frontal; *mx*, maxilla; *p*, premaxilla; *q*, quadrate; *z*, zygomatic.

foramen and the small parietals sometimes reached the anterior border of the orbit. The fused frontals form most of the cranial roof, the elongate maxillæ most of the beak. The large antorbital vacuity is confluent with the naris in some genera. The orbits, sometimes with sclerotics, are separated from the

temporal fossa by a three-branched postfrontal, one ramus meeting the squamosal to form the upper arcade. The orbits are bounded in front by prefrontal and a process from the zygomatic. The large quadrate is fixed by squamosal above and pterygoid below; no transversum occurs. The halves of the lower jaw are fused at the symphysis. Each half consists of the typical six bones, sutures persisting in some genera. Some species were toothless; others have thecodont teeth in the margins of the jaws. Traces have been found of a slender hyoid.

DINOSAURIA have a relatively small skull, which, in Saurischia, was carried nearly in line with the vertebral column; in Ornithischia nearly at right angles with it. The cranium of Theropoda is not completely ossified. Both temporal fossæ are present as is an antorbital vacuity of varying size, smallest or lacking in Ornithischia. The sutures between the bones are frequently indistinct. Sometimes the foramen magnum was bordered by the four occipitalia, some-
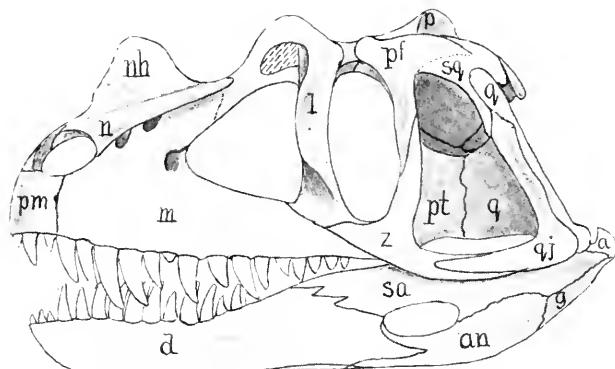
FIG. 181.—Skull of *Ceratosaurus* (Gilmore, '15). *a*, articulare; *an*, angulare; *d*, dentale; *m*, maxilla; *n*, nasal; *nh*, nasal horn-core; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sa*, surangulare; *sq*, squamosal; *z*, zygomatic, *g*, goniale.

times by exoccipitals alone, these bones sometimes being distinct, sometimes more or less completely fused with the supraoccipital, and always with the opisthotics, forming a parotic process on either side. No parietal foramen is known. The frontals are paired, and in Ceratopsia each has a horn core (large in some genera) and a third on the nasals. The orbits are large, and the nares, usually far anterior, often lie between maxillæ, premaxillæ and nasals, but in Ceratopsia, where they are very large, they are bounded in front by a **rostral bone,** not known outside this group. The rather large premaxilla may bear teeth or be edentulous, the teeth of both jaws being in alveolar grooves or thecodont.

The imperfectly known cranial floor, was somewhat like that of Rhynchocephals, the palatines meeting in the middle line. Some have the pterygoids approximate and some have an epipterygoid. The large quadrate is united by

suture to squamosal, quadratojugal and pterygoid, but may have had slight motion in some species. It extends downwards and forwards so that in some the hinge of the lower jaw is beneath the orbit. All, except the Ceratopsia, lack a coronoid process. The tip of the lower jaw of Ornithischians (fig. 182, *B*) is formed by a **predentary bone,** peculiar to this group.
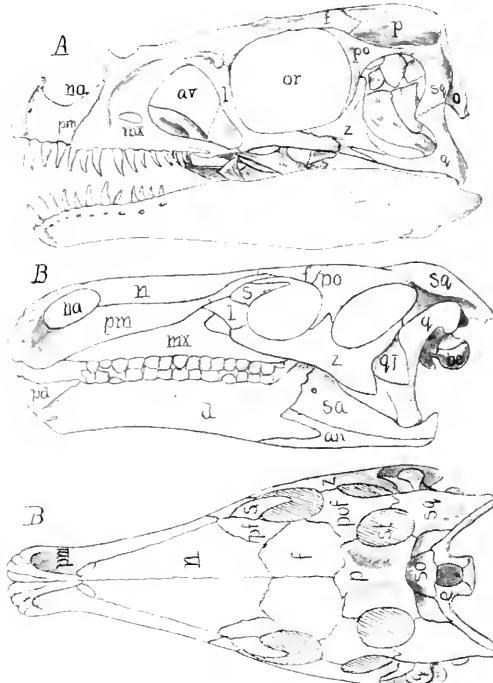
FIG. 182.—Skulls of Dinosaurs. *A, Ornitholestes hermanni* (Osborn, '16); *B, Camptosaurus* (Gilmore, '09). *an*, angulare; *av*, antorbital vacuity; *d*, dentale; *e*, exoccipital; *f*, frontal; *l*, lacrimal; *mx*, maxilla; *n*, nasal; *na*, naris; *o*, opisthotic; *or*, orbit; *p*, parietal; *pd*, predentary; *pf*, prefrontal; *pm*, premaxilla; *po*, postfrontal; *q*, quadrate; *sq*, squamosal; *st*, supratemporal fossa; *z*, zygomatic.

AVES.—The bird's skull is most closely related to that of reptiles, the resemblance being most marked in the single occipital condyle, largely or wholly on the basioccipital; the suspensorial quadrate, the usual antorbital vacuity; and the tropibasic chondrocranium. But there are marked differences, the most noteworthy being correlated with the greater development of cerebrum and cerebellum which has caused a great vaulting of the cranial roof and a widening of its sides, resulting in the entrance of the squamosal into the wall of the cranial cavity, between parietal, exoccipital and prootic. The backward extension of the brain and the non-horizontal neck have

changed the position of the cranial base to an oblique plane so that condyle and foramen magnum look obliquely downwards, and the skull is usually carried at nearly a right angle to the axis of the body. Less prominent is the absence of several bones, common in reptiles, among them transversum, postfrontal, postorbital and epipterygoid. It is not certain that none of these appear in ontogeny, fusing later with other elements.

The cranial bones fuse early, except in Ratites, with almost complete obliteration of most sutures, especially in the brain case. Frequently a suture persists between frontals and nasals which allows motion of the tip of the upper jaw (fig. 183). The strepto-stylic quadrate is very mobile and the arrangement of skeletal parts is such that depression of the lower jaw forces the distal end of the
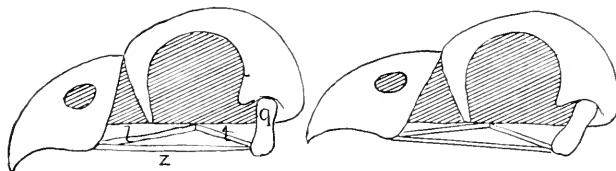
FIG. 183.—Diagram of movement of upper jaw of birds (Boas). *l*, palatine; *t*, ptery-goid; *z*, zygomatic bar.

quadrate forwards and this motion is transmitted forwards, both by the zygomatic arch and by the palatine-pterygoid series (which slide on the rostrum), to the upper jaw in front of the hinge between nasals on one side, and frontals and mesethmoid on the other. In this way the anterior part of the beak is elevated, increasing the gape. This mobility of the upper jaw is especially well developed in parrots, owls and goatsuckers.

All modern birds lack teeth, but their germs are known in some embryos. Some extinct birds had them well developed. Modern birds have the beak enclosed in horny sheaths, variously developed and largely supported on premaxillæ and dentalia. The orbits are very large, those of the two sides being separated by a very thin interorbital septum, variously chondrified or ossified, or reduced to membrane. Except in parrots, the orbit is continuous with the single temporal fossa, this bounded laterally by the lower arcade of diapsid reptiles which is always present. The orbits, except in owls, look laterally, and the lower border is complete except in parrots. Sclerotic bones are common.

The history of the chondrocranium is partly known and the following account is tentative. The basal plate (fig. 184, *b*) arises as a continuum of notochord, parachordals and three occipital vertebræ, the posterior the most prominent, while in some birds the arch of the first vertebra arises independently and forms the metotic pillar, with nerves IX and X between it and the otic capsule. The foramen for the nerves is completed in the usual way, and is later divided by a process from the basal plate into glossopharyngeal and jugular foramina. The synotic tectum chondrifies separately, soon uniting with the capsules and the dorsal ends of the fused occipital vertebræ, which become shortened and telescoped, accompanying the change in the plane of the foramen magnum, the tectum becoming nearly vertical.
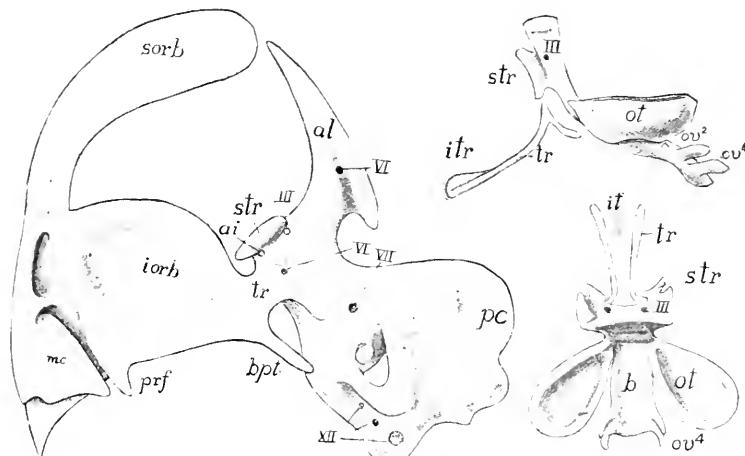
Fig. 184.—Earlier (right) and later (left) stages of chondrocranium of *Tinnunculus* (Suschkin, '99). *al*, 'alisphenoid' cartilage; *ai*, foramen for internal ophthalmic artery; *b*, basal plate; *bpt*, basipterygoid process; *iorb*, interorbital septum; *itr*, intertrabecula; *mc*, middle concha of nose; *ot*, otic capsule; *ov*, occipital vertebræ; *pc*, posterior semicircular canal; *sorb*, supraorbital bar; *str*, supratrabecula (with *al*, forms sphenolateral); *tr*, trabecula.

The prechordal parts appear later than the chordal. As a result of the cephalic flexure, the trabeculæ (formed independently) are at first nearly at right angles with the basal plate, the angle soon flattening to about 160°. Some birds have a separate intertrabecular plate between the anterior ends of the trabeculæ, this forming the ethmoid region; in others the trabeculæ unite directly to a trabecula communis which reaches to the hypophysis where the two trabeculæ separate, forming the sides of the hypophysial fenestra, and joining the anterior margin of the basal plate.

Several chondrifications occur in the interorbital region (fig. 184), the relations of which are uncertain. An interorbital septum grows up from the common trabecula, dividing dorsally into supraseptal plates. The septum extends back to the optic nerves which pass on either side of it. In *Tinnunculus* a large cartilage (*sorb*) extends back from the nasal region as two diverging

plates which are probably the anterior parts of the marginal tæniæ. Behind the optic nerve, and connected with the basal plate, is an ascending cartilage which, as it is perforated by the third, and sometimes by the ophthalmic branch of the fifth nerve, is clearly sphenolateral. Later this grows still farther dorsally and joins the otic capsule behind, this part apparently being the preotic pillar. This posterior part suddenly diverges, enlarging the cavity for the brain, which is made still larger by the lowering of the floor between them to the trabecular level. An interesting feature in *Tinnunculus* is the existence of two islands of procartilage in the cranial roof, on the hinder side of the pinealis.
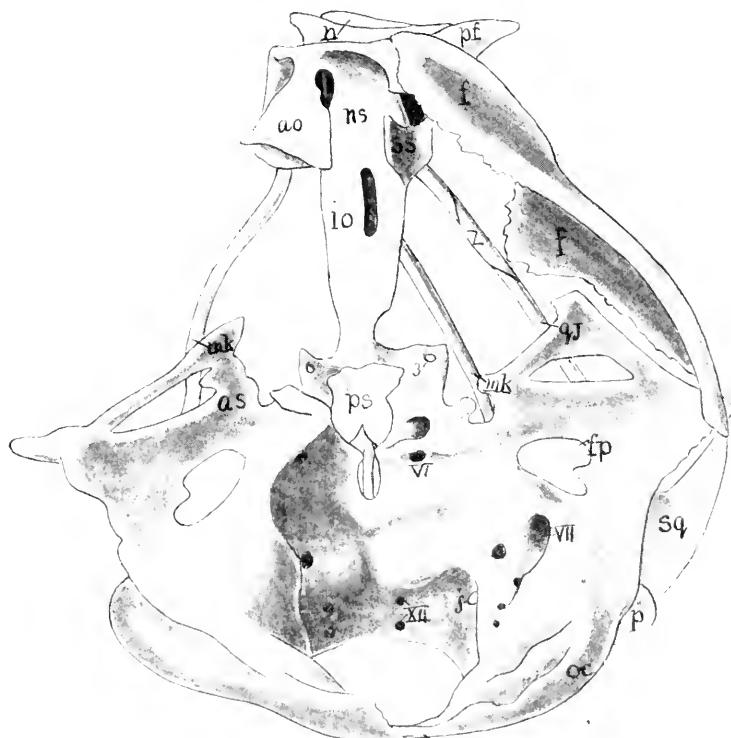
Fig. 185.—Chondrocranium of chick (Tonkoff's model, in Gaupp, '05). *ao*, antorbital process; *as*, alisphenoid cartilage; *f*, frontal; *fp*, preotic foramen; *io*, interorbital septum; *j*, jugular foramen; *mk*, Meckelian; *n*, nasal; *ns*, nasal septum; *oc*, occipital region; *p*, parietal; *pf*, prefrontal; *ps*, parasphenoid; *qj*, quadratojugal; *sq*, squamosal; *ss*, supraseptal plate; *z*, zygomatic.

The nasal septum is a continuation of the common trabecula or of the intertrabecular cartilage and is continued forwards by the prenasal cartilage. Two fenestræ appear in the septum, one soon closing; the posterior, just behind the nasal sacs, enlarges in many birds so that the septum is interrupted except at its base, thus forming a cranio-facial fissure, important in the later mobility of the beak (p. 170), the whole nasal labyrinth participating in the motion.

An antorbital plate arises from the side wall just in front of this fissure and forms the hinder wall of the capsule, while later, the lateral wall and roof arise as continuations of the median septum (in some the lateral wall starts as a separate chondrification). Internally the capsule consists of an anterior atrium and a wider posterior part with two conchæ (turbinals), ingrowths from the lateral wall.

The mandibular arch consists of quadrate and Meckelian. The former lies close to the otic capsule and consists of a body with a pterygoid process, directed anteriorly and medially, which is soon reduced. An otic process appears a little later, extending to the region of the anterior semicircular canal, differentiating later into two parts for articulation with the capsule and with the squamosal respectively. The lower end of the quadrate has two condyles to fit corresponding surfaces on the head of the Meckelian. The two Meckel's cartilages are widely separate anteriorly at first, gradually growing together, in *Melopsittacus* by the intervention of a copular cartilage.
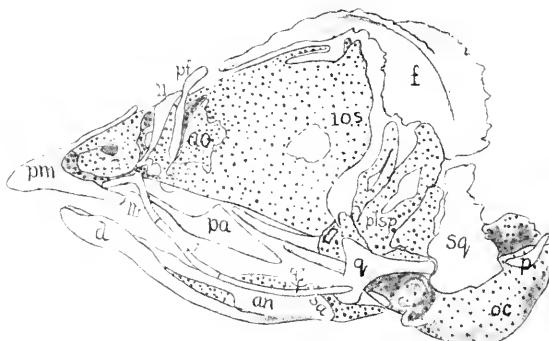
Fig. 186.—Later chondrocranium of chick with membrane bones (Tonkoff, in Gaupp, '05). *an*, angular; *ao*, antorbital cartilage; *d*, dentale; *f*, frontal; *ios*, orbital septum; *m*, maxilla; *n*, nasal; *oc*, otic capsule; *p*, parietal; *pl*, palatine; *pf*, prefrontal; *plsp*, sphenolateral; *pm*, premaxilla; *q*, quadrate; *qj*, quadratojugal; *sa*, surangulare; *sq*, squamosal; *z*, zygomatic.

The accounts of the development of the hyoid apparatus are contradictory and leave many points uncertain. The hyoid arch (fig. 187, *B*) arises as two separate parts on either side, one closely associated with the cranium, the other in the pharyngeal floor. The latter adjoins a median copula; statements differ as to its fate. Usually it is said that the copula forms a small projection (entoglossum) near the anterior end of the apparatus, but others say that this arch unites with the copula, and in parrots furnishes the loop on the upper side of the copula. This statement also recognises a pair of separate **paraglossal cartilages** near the end of the copula, which, with the copula, form the entoglossum which often is bifid at the tip. The larger cornu arises from the first branchial arch and divides early (usually) into two elements (sometimes three), variously called hypo- and ceratobranchial or cerato- and epibranchial. The copula sometimes has connected with it posteriorly a pair of subcopular cartilages which unite and give attachment to muscles.

The dorsal half of the hyoid arch rests on the otic capsule and plays a part in the development of the columellar apparatus, concerning which accounts differ widely. The columella itself arises from this arch, the upper part (stylo-hyal) forming the infrastapedial process. The columella itself (fig. 188) has two distal processes, supra and extrastapedial, which later unite at their ends, thus completing the ring, characteristic of birds, through which a blood vessel passes. Some recognize two parts in the stapedial, one (otostapes) derived from the capsular wall, the other (hyostapes) coming from the hyoid arch, but later accounts deny any contributions from the capsule.
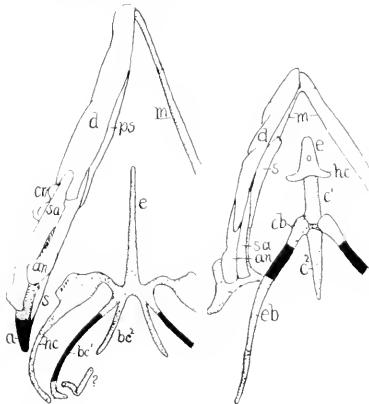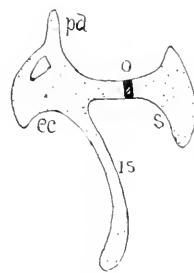
Fig. 187.   Fig. 188.

Fig. 187.—Developing lower jaw and hyoid apparatus of (A) *Lacerta*, and (B) chick (Gaupp, '05), cartilage bones black. *a*, articulare; *an*, angulare; *bc*, branchial cornu; *c*, copula; *cb*, ceratobranchial; *cr*, coronoid; *d*, dentale; *e*, entoglossum; *eb*, epibranchial; *hc*, hyoid cornu; *m*, Meckel's cartilage; *ps*, presplenial; *s*, splenial; *sa*, surangulare.

Fig. 188.—Beginning ossification (black) of columella of *Tinnunculus* (Suschkin, '99). *ec*, *pd*, extracolumella and dorsal process of otostapes; *is*, infrastapedial; *o*, bone; *s*, stapedial plate of hyostapes.

In the adult avian skull replacement of cartilage is almost complete, it persisting only in the ethmoid region, and, as stated above, most of the cranial bones, cartilage and membrane, are so completely fused that sutures are obliterated. All four occipitalia are ossified, the basioccipital, which bears most or all of the condyle, last. All four unite without trace of suture and the basioccipital fuses with basisphenoid and opisthotic.

The basisphenoid has two ossification centres and extends farther forwards than in other Sauropsida, including in its extent a part of the interorbital septum. It is somewhat cruciform and supports most of the lower surface of the brain. It frequently develops basi-pterygoid processes (long in some Euornithes, but usually low articular facets) for articulation with the pterygoids. Owing to a gap

between basicranial and hypophysial fenestræ, the dorsum sellæ cannot ossify in the usual manner, but is formed by growth from below. The alisphenoids are associated with the basisphenoid, ossifying in the preotic pillars by two or three centres in each. These bones, which ossify late, form the greater part of the posterior wall of the orbit and largely close the brain cavity laterally and in front. The second and third rami of the fifth nerve make their exit between the alisphenoid and the otic capsule, passing either together or through separate foramina. The alisphenoid fills the gap between orbitosphenoid, interorbital septum, petrosal, frontal and squamosal, the latter usually separating it from the parietal. The presphenoid has two centres in the base of the interorbital septum, the resulting bone being small and fusing with the adjacent bones, it and the underlying part of the parasphenoid uniting as the sphenoidal rostrum. The orbitosphenoid ossifies from a centre in the supraseptal plate, and extends downwards, the resulting bone being small. Between it and the alisphenoid are the exits of nerves II, III, IV, and VI, and the ophthalmic branch of V, some of which may have separate foramina in the adult, some passing out with the optic nerve through the orbital fissure. When a separate optic foramen occurs, it is near the base of the bone.

The olfactory nerve leaves the main cranial cavity at the junction of frontals and orbitosphenoid, runs forwards in the groove between the supraseptal plates to the ethmoid region. There are several centres in the nasal septum and wall of the nasal capsule, and a separate centre in the antorbital plate These form a mesethmoid and a pair of ectethmoids which soon
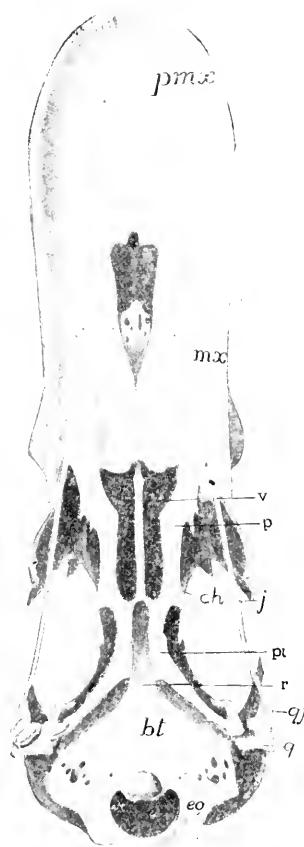
FIG. 189.—Palate of duck. *bt*, basitemporal plate; *ch*, choana; *eo*, exoccipital; *j*, zygomatic; *mx*, maxilla; *p*, palatine; *pmx*, premaxilla; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *r*, rostrum; *v*, vomer.

unite to a common ethmoid. There is sometimes a separate centre in the prenasal cartilage, sometimes the cartilage degenerates. At first the ethmoid is visible on the outer surface of the cranium between frontals and nasals, permanently so in ostriches; elsewhere it becomes covered by growth from maxilla and premaxillæ.

Three bones develop in the otic capsule—pro-, epi-, and opisthotic (fig. 190)—and there may be other centres of uncertain homology. The prootic extends far back on the lateral and medial sides, encloses the seventh nerve and joins the opisthotic (mastoid) behind and the alisphenoid in front above the foramen lacerum. The epiotic, ossifying late, is small and fuses with the supra- and upper part of the
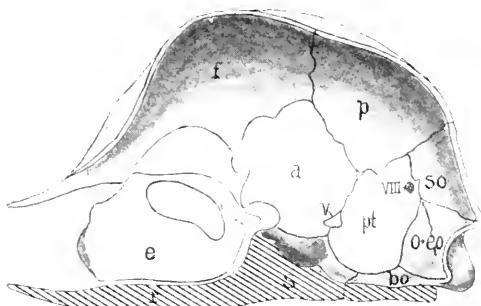
FIG. 190.—Interior of cranium of ostrich (Pouchet et Beauregard, '89). *a*, alisphenoid; *bo*, basioccipital; *e*, ethmoid; *f*, frontal; *o + eo*, opisthotic and exoccipital; *p*, parietal; *pt*, petrosal; *r*, rostrum; *s*, sphenoid; *so*, supraoccipital.

exoccipital. The opisthotic arises between epiotic and exoccipital, fusing with the latter and sometimes (gulls) entering the border of the foramen lacerum. Vestibular and cochlear fenestræ lie between pro- and opisthotic. All of the otica usually fuse to a petrosal (periotic) bone which lies between basioccipital and basisphenoid below, alisphenoid and squamosal in front, the latter largely overlapping it in front, and the parietal and occipitals above and behind.

The parietals, always small, arise laterally on the otic capsules and eventually form the posterior part of the cranial roof, there being in some birds a gap between them and the supraoccipital. Anteriorly they reach the frontals which form most of the roof and which arise far laterally, and extend from the nasal roof back to the alisphenoids. Each has a broad ventral postorbital process extending down so far that it forms a part of the orbito-temporal wall. Sometimes this part ossifies separately and may represent the postfrontal of

reptiles which otherwise is absent. Except when the supraorbitals are present, the frontals form most of the supraorbital border.

The nasals, arising on the hinder part of the nasal capsules, bound the nares more or less completely, the shape of those openings having some systematic importance. Usually the nasals fuse with frontals, ethmoid, maxillæ and premaxillæ, but when the beak is mobile (p. 170) a joint comes between frontals and nasals.

The premaxillæ, forming the greater part of the beak, arise from centres on the prenasal cartilage and are always fused in the middle line, and laterally to the maxillæ. Each has palatine, lateral and ascending processes, the latter reaching the frontal. The maxillæ,
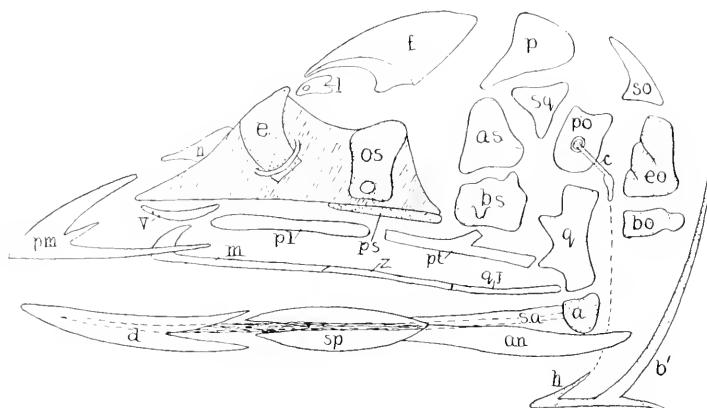
Fig. 191.—Schema of bones in bird skull (Newton, '93–96); cartilage bones dotted, cartilage lined obliquely. *a*, articulare; *an*, angulare; *as*, alisphenoid; *b*[1], 1st branchial; *bo*, basioccipital; *bs*, basisphenoid; *c*, columella; *d*, dentale; *e*, ethmoid; *eo*, exoccipital; *f*, frontal; *h*, hyoid; *l*, lacrimal; *m*, maxilla; *n*, nasal; *os*, orbitosphenoid; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *ps*, rostrum (?presphenoid); *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sp*, splenial; *sq*, squamosal; *v*, vomer; *z*, zygomatic.

pyramidal in shape, vary greatly in size, being the most conspicuous bones, the premaxillæ excepted, in herons, while they are very small in fowl. They lie ventral to the posterior part of the nasal capsule with which their palatine processes are fused. Each articulates behind with the (usually present) zygomatic which forms the anterior part of the zygomatic arch. It and the following quadratojugal are long and slender, the latter articulating with the quadrate, the arch playing a part in transfer of motion from the quadrate to the beak.

There is usually a prefrontal at the anterior border of the orbit, its varying relations being used by systematists. It is usually per-

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forated for the lacrimal duct and orbital gland, which led to its being regarded as a lacrimal, but it is probably the homologue of the reptilian prefrontal, although it may contain supraorbital elements. Supraorbitals, as one or more distinct bones, are present in several birds (Raptores, some fowl, crane, ostrich, *Tinamus* and *Arboricola* have several) loosely attached to frontal or prefrontal. Some birds have an infraorbital adjoining the zygomatic or descending process of the prefrontal.

The squamosal, on the anterolateral otic region, forms a part of the cranial and usually of the postorbital wall. It often has a descending process which separates orbit and temporal fossa and (some parrots) continues forwards, bounding the orbit below. It is peculiar in not connecting with the zygomatic arch.
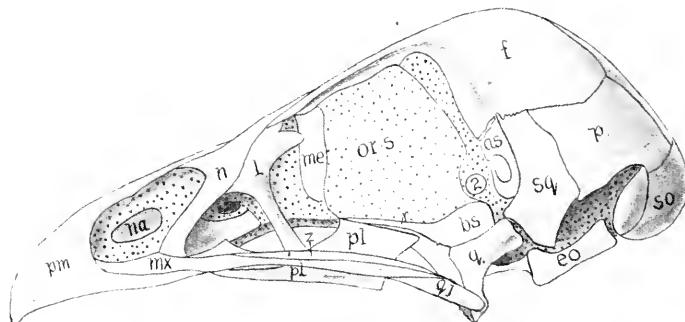
FIG. 192.—Cranium of young *Buteo* (Butschli, '10); cartilage stippled. *as*, alisphenoid; *bs*, basisphenoid; *eo*, exoccipital; *f*, frontal; *l*, lacrimal; *me*, mesethmoid; *mx*, maxilla; *n*, nasal; *na*, naris; *ors*, orbital septum; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *q*, quadrate; *qj*, quadratojugal; *r*, rostrum; *so*, supraoccipital; *sq*, squamosal; *z*, zygomatic; *2*, exit of optic nerve.

Birds never have the closed palate of many reptiles (fig. 189). The parasphenoid arises on the lower hinder part of the cranium by three centres, one a little in front of the hypophysial fenestra, the paired centres being ventral to the lateral parts of the basal plate and otic capsules, these latter forming the bone formerly called the **basitemporal.** The anterior part closes the hypophysial fenestra and fuses with the presphenoid, forming the rostrum. It also fuses with the basitemporal parts which unite so firmly with the basisphenoid that they cannot be separated.

The vomer, variable in size (sometimes absent, and small except in Ratites) arises from paired centres, the two halves remaining separate in Picidæ. It lies on the lower side of the interorbital

septum, and is usually visible between the palatines. These latter are long and flat, and usually have an articular surface which forms a sliding joint on the rostrum, while the posterior part articulates with the pterygoid, the anterior being connected immovably with the premaxilla (except in Ratites) and borders the choana. The pterygoid articulates with the quadrate and sometimes with the basipterygoid process of the alisphenoid, sometimes with the rostrum in front.

The palatal structure has been invoked as a basis of classification of birds. Originally four types were recognized (Huxley): **dromæognathous, schizogna-thus, ægitognathous** and **desmognathous.** More recently birds have been
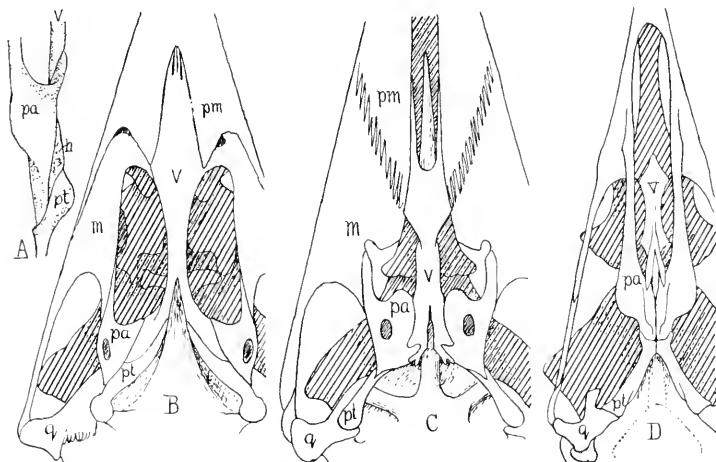
FIG. 193.—Palatal regions of (*A*) *Corvus*, (*B*) *Dromæus*, *C*, *Rhea*, and (*D*) *Rissa* (Pycraft, '01). *h*, hemipterygoid; *m*, maxilla; *pa*, palatine; *pm*, premaxilla; *pt*, pterygoid; *q*, quadrate; *v*, vomer.

separated into two great groups, each with subdivisions. In dromæognaths the united vomer is large and overlaps (ultimately fusing with the anterior ends of) the pterygoids so that motion is impossible between them. The pterygoids and palatines do not meet the rostrum, and the palatines, which do not meet the premaxillæ, articulate with the maxillæ. *Dromæus* (fig. 193, *B*) has the anterior end of the vomer entire, concealing the rostrum, while the broad hinder end of the palatine meets the lateral end of the vomero-pterygoid (Palæognathæ). From this the tendency is for the palatines to meet ventral to the vomero-pterygoid junction (pterygoid sometimes meeting only vomer; palatine and vomer in others) while a division of the vomer in front allows the rostrum to be seen (true Dromæognaths). In Neognathæ the palatines meet behind in the middle line, supporting the vomer between them, while there is a moveable

joint between palatine and pterygoid, formed by a part (**hemipterygoid**) of the pterygoid fusing with the palatine (fig. 193, *A*) and separating from the pterygoid with a joint between.   The palatines have lost their connexion with the maxillæ and now meet and fuse with the premaxillæ.   *Tinamus*, is between the two groups, but nearer the Dromæognaths.

In Ratites the quadrate has a single head (partly divided in a few) for articulation with the otic capsule; in Euornithes it has a double head, one for articulation with the capsule, the other with the squamosal.   There is a strong medial and ventral process extending towards the pterygoid, while the bone connects with both pterygo-palatine and zygomatic bars.   Its mobility was noted above.

The lower jaw (fig. 191) has an articulare behind, ossified in Meckel's cartilage and there is a mento-Meckelian at the tip of the jaw.   The usual Sauropsidan bones form around the cartilage.   The dentalia form most of the jaw, followed medially by one or two splenials.   There is a surangulare or coronoid on the upper side which affords insertion for the masseter muscle, while, lower, the angulare, together with the articulare afford places of insertion of the digastric.   There is often a vacuity in the side wall of the jaw. The dentalia of the two sides fuse in all modern birds, but in some fossils the two halves of the mandible were apparently movable.

The hyoid apparatus (fig. 187) is most like that of Chelonia, of existing reptiles, in general appearance, but several points of homol-ogy are uncertain.   The structure consists of a long and slender body composed of two copulæ, often distinct in the adult (then known as **basihyal** in front, **urohyal** behind).   In front of the first is a single or paired **entoglossum,** while between the two copulæ a pair of greater cornua are attached.   These last are part of the first branchial arch and are usually two- (sometimes three-) jointed. They reach their greatest development in Picidæ and Trochilidæ where they curve around the base of the cranium and terminate on its upper surface near the nares.

If the development described above (p. 173) in *Melopsittacus* hold, then the basal parts of the hyoid are lost in the loop in that genus, while the hinder parts of the entoglossum, usually called the hyoid cornua, are formed from the para-glossæ, which certainly are not parts of the hyoid arch.   The entoglossum is either simple or shows traces of its paired origin, being either two-horned or perforate.   The urohyal extends far behind the attachment of the greater cornua.

MAMMALIA.—The skulls of mammals possess especial interest since they include that of man, and consequently have been studied more than those of any other class; yet there are many points awaiting solution. The number and arrangement of the bones is fairly constant, and yet there is as great a variety of form as in any non-mammalian group. Then the question of the origin of the Mammalia receives more information from the skull than from any other structure.

For many years the paired occipital condyles of mammals were thought to indicate an Amphibian ancestry for the class, but it was shown later that these could be derived from the tripartite condyle of certain reptiles by the recession of the basioccipital portion. The chondrocranium, while lacking an interorbital septum, can be regarded as tropibasic, the loss of septum being the result of the great size of the anterior part of the brain, but it must be recalled that many Teleosts have tropibasic crania. Another feature of importance in this connexion is the comparatively entire oral roof, the hard palate (palatine processes of premaxillæ, maxillæ and palatines) being paralleled only in monimostylic reptiles. The bearing of the quadrate on the problem of mammalian origin will be alluded to later.

There are other features of the skull which are the result of the large brain of even the lowest members of the class. In other Vertebrates, birds excepted, brain and spinal cord are in a straight line and the parts of the brain are small. Mammals have cerebrum and cerebellum greatly enlarged relatively to other parts. As the lower side of the brain is held in position by the exit of nerves and the entrance of blood vessels through the skull, all expansions of the brain must be dorsal to this, causing a widening and vaulting of the lateral and roofing walls, the extent of which is usually directly related to the size of the brain. (Some mammals—elephants, Ruminants and Edentates—have cavities and cells in the diploe which increase the size of the brain case.) The increase in size of the cranial cavity affects the ali- and orbitosphenoids, inconsiderable elements in lower Vertebrates, and, as in birds, has brought the squamosal into the cranial wall, and also has forced these bones and the otica (vertical in lower groups) largely to the cranial floor. The extension backwards of the brain has caused a change in the position of the base of the skull and the foramen magnum, a change, while

hardly noticeable in lower mammals, is marked in the higher where
the foramen is on the ventral side of the skull.   Growth of the cere-
brum forwards causes it to override the olfactory nerves so that the
olfactory foramina are vertical in the higher groups, the anterior
part of the cranial cavity lying dorsal to the olfactory labyrinth.
The dorsal extension of the brain causes a vaulting of the roof,
paralleled only in birds.

The number of bones is smaller than in most lower classes, the
reduction being partly due to fusion, partly to absolute loss.   Thus
the otica are fused to a **petrosal bone** and this is often united with
squamosal and tympanic, forming a **temporal bone.**   The sphenoi-
dalia unite to a single **sphenoid bone** (sometimes two), and only a
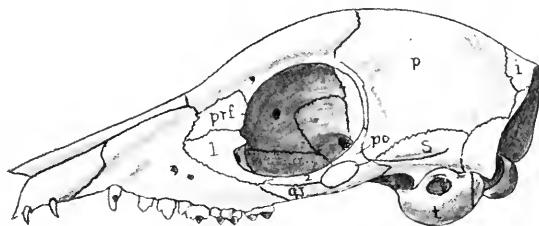
FIG. 194.—Cranium of *Tupaia* (Wortmann, '20) showing bones possibly to be
interpreted as he has. *i*, interparietal; *l*, lacrimal; *p*, parietal; *po*, postorbital
prf, prefrontal; *qj*, quadratojugal; *s*, squamosal; *z*, zygomatic.

single bone, largely dentale, is recognizable in either half of the adult
lower jaw.   Of actual cases of loss, the supratemporal, pre- and post-
frontal, postorbital and quadratojugal may be cited, no traces of
these having been seen.[1]

Most important of the differences between the skulls of mammals
and those of lower Vertebrates is the disappearance of the quadrate
from the suspensorial apparatus; a position it occupies from Elasmo-
branchs to birds; in mammals it functions as an element of the
sound-transmitting structures of the middle ear, the lower jaw in
mammals being articulated with the squamosal, and the quadrate
is removed from the hinge.

[1] The recent statement of Wortman ('20) that pre- and postfrontal and quadrato-
jugal bones (fig. 194) occur in adult mammals needs confirmation. Monotremes
have an element in the position of the postfrontal which may be this bone.   It is pos-
sible that the mammalian lacrimal is the same as the reptilian prefrontal, but this has
been noted (p. 139) as being at least doubtful.   In a few cases a bone has been
described (Ameghino, Fuchs) in the zygomatic arch in the position of a quadratojugal,
but it has not been shown to be such.

It is unfortunate that we have no adequate accounts of the earliest stages of the cartilage skull. The chondrocranium arises in pre- and postchordal parts. The basal plate is formed by the parachordals with the addition of three occipital vertebræ as in all Amniotes, so far as known, these fusing early with the parachordals, a basicranial fenestra occurring occasionally. The jugular foramen is formed as elsewhere, between the first occipital vertebra (postotic pillar) and the otic capsule and is closed dorsally by growth from these. Dorsally each half of the postotic region continues into a broad plate dorsal to the foramen magnum, and is at first distinct from the synotic tectum which arises as a discrete cartilage.

The otic capsules, from the first, lie in the cranial floor, each having its major axis inclined medially inwards and forwards. Sometimes they arise apart from the basal plate to which they become attached in various ways in different
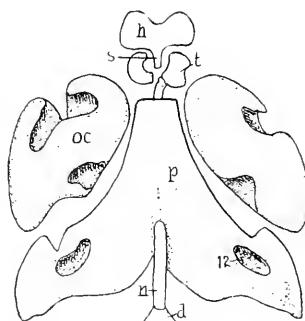
FIG. 195.—Chondrocranium of 14 mm. human embryo (Fawcett, '19). *d*, dens epistrophei; *h*, hypophysis; *n*, notochord; *oc*, otic capsule; *p*, parachordal plate; *s*, stalk of hypophysis; *t*, trabecula; *12*, hypoglossal canal.

mammals. At first floor and roof of the capsules are separate. A ('parietal') plate of cartilage arises from the upper posterior part of each capsule and passes behind into the tectum, and is usually connected in front by an orbito-parietal commissure with the orbitosphenoid, and thus is a marginal tænia.

It is uncertain whether the trabeculæ arise separately from the basal plate; if they do, they unite early. The bars and the prehypophysial common trabecula are short and the hypophysial fenestra is nearly closed, there being for a short time a narrow opening for the hypophysial stalk. A small sphenolateral cartilage (**ala temporalis**—sometimes a separate chondrification) passes laterally from the side of the trabecula, with a wide gap between it and the otic capsule, and bears on its lower posterior border a small, ventrally directed process which later forms the lateral lamella of the pterygoid process of the sphenoid bone.

The third branch of the fifth nerve passes through the gap (foramen lacerum) between sphenolateral (alisphenoid) and otic capsule, but is soon surrounded by cartilage which connects with the alisphenoid, thus outlining the foramen ovale. The other branches of the trigeminus pass forwards, medial to the alisphenoid, and then out, at first through the orbital fissure. Later they are enclosed in a foramen rotundum, formed in the same way as the f. ovale.

It is stated that there are no true trabeculæ in mammals and that the cartilage here called alisphenoid is not homologous with the alisphenoid of Sauropsida, but may be the same as the basipterygoid processes of reptiles. The first is supported by the fact that the cartilages are medial to the carotid arteries. The non-homology of the alisphenoids is based on the fact that these cartilages in mammals lie lateral to the fifth nerves, medial to them in other Vertebrates. Neither reason seems sufficient to establish these contentions when the variabil-

FIG. 196.—Chondrocranium of 12 mm. *Tatusia 9-cincta* (Fawcett, '21). *ao,* ala orbitalis; *at,* ala temporalis; *c,* carotid foramen; *co,* cochlear part of basal plate; *e,* endolymph foramen; *eo,* exoccipital; *et,* ethmoturbinal; *h,* hypophysial canal; *j,* jugular foramen; *m,* Meckelian; *n,* notochord; *oc,* otic capsule; *pc,* parachordal; *pp,* parietal plate; *ps,* anterior paraseptal cartilage; *s,* orbital-nasal septum; *tna,* anterior nasal tectum; II, optic foramen; XII, hypoglossal foramen.

ity of blood vessels, and the shifts which must accompany the great increase in the mammalian brain are considered. Hence the older (and more natural) interpretation of parts is retained here.

The orbitosphenoid cartilage (fig. 197), connected with the pre-sphenoid region, is much larger than the alisphenoid, even in the early stages of man where the reverse holds for the adult. The base of each cartilage becomes perforated for the optic nerve (originally

in the orbital fissure) by a separate outgrowth from the trabecula which unites with the orbitosphenoid cartilage. A marginal tænia connects the orbitosphenoid with the otic capsule, and a spheneth-
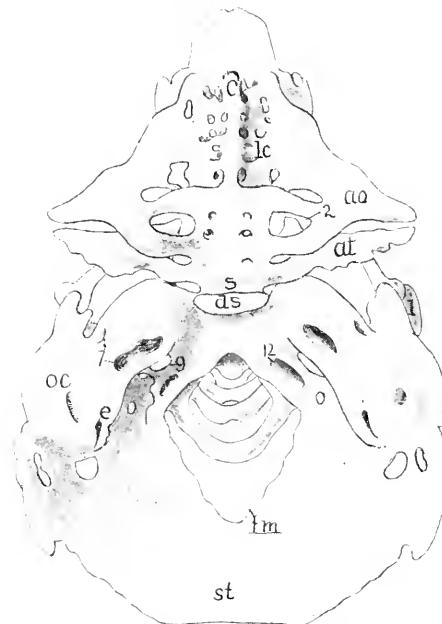
FIG. 197.—Chondrocranium of 80 mm. human embryo (Gaupp, '05). *ao*, ala orbitalis; *at*, ala temporalis; *c*, crista galli; *ds*, dorsum sellæ; *e*, opening of endolymph duct; *fm*, foramen magnum; *lc*, lamina cribrosa; *oc*, otic capsule; *s*, sella turcica; *st*, synotic tectum.
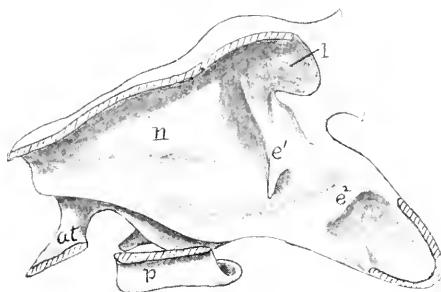
FIG. 198.—Interior of nasal capsule of 23 mm. cat embryo (Terry, '17). *e*, ethmo-turbinals 1 and 2; *at*, anterior transverse process; *l*, lateral recess; *n*, naso-turbinal; *p*, paraseptal cartilage.

moid bar unites it with the nasal capsule. Both ali- and orbito-sphenoids extend laterally from the trabeculæ (the result of the large brain), and no interorbital septum is formed.

Notwithstanding the greater complexity, broad homologies can be traced between the nasal capsules of mammals (fig. 198) and reptiles. The capsules of the two sides are separated by a vertical septum which extends back to the olfactory fenestra, lateral to the septum, through which the first nerve enters the olfactory region. At first each fenestra is simple in all mammals, and remains so in Monotremes and some apes. Elsewhere it becomes divided into numerous openings for separate branches of the nerve, then this part is called the **lamina cribrosa,** the name (and also the word ethmoid) referring to this sieve-like condition. A roof of cartilage extends laterally from the top of the septum over each nasal sac, and bends downwards to form the lateral wall.

In lower mammals the nasal cavities are in front of the cranial, but in the higher the cranial overlaps the nasal, resulting in a change in the position of the lamina cribrosa from nearly perpendicular to approximately horizontal.

When bones begin to develop in the skull, gaps (fontanelles) are common in the fetal roof and sometimes persist in the adult. Most common of these are the occipital fontanelle in the **lambdoid suture** between the supraoccipital and the parietals; and the frontal fontanelle in the **coronary suture** between parietals and frontals. Less common is the **asterion** on either side between parietal, squamosal, and occipital, and the **pterion fontanelle** between frontal, parietal and alisphenoid. Vacuities are rare in the adult, exceptions being most common in Ruminants between frontal, lacrimal and maxilla.

The shape of the skull varies somewhat with age, this being most marked in Primates, less in Carnivores. Cranial parts predominate over facial in higher groups, this not always caused by brain development, for it also occurs in elephants, Ruminants and Edentates as the result of cavities in the bones. Strong jaw muscles tend to cause a crest in the sagittal line of the roof of the skull, this affording greater surface for muscular origin. It is noteworthy that, aside from the ossicula auditus and the lower jaw, the bones of the adult skull are immoveably united by sutures, these being obliterated to the greatest extent in Monotremes.

The number of cartilage bones (fig. 199), distinct at first, is greater than in modern reptiles; some, especially in the ethmoid and interorbital regions, being without homologues in that group, but are new acquisitions of mammals.

Distinct occipitalia often persist in the adult, but as often all fuse to a single occipital bone with which the interparietal (scarcely known elsewhere above primitive reptiles) may unite. This occip-
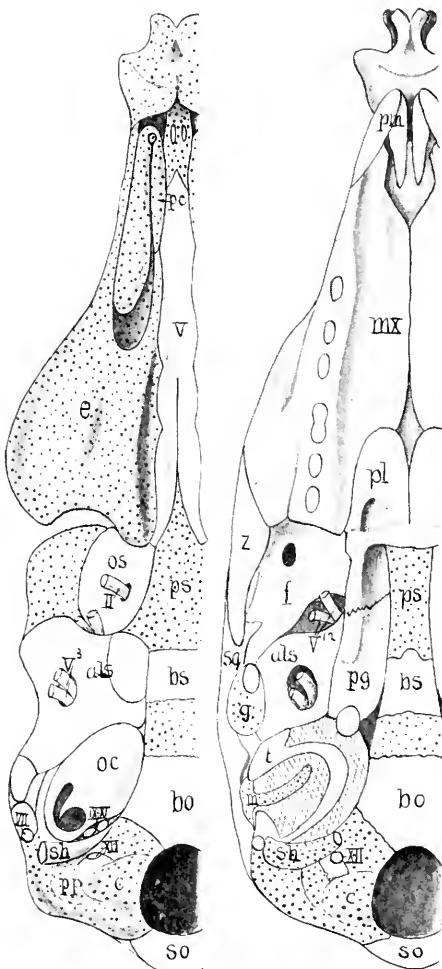
FIG. 199.—Ventral views of developing cranium of *Orycteropus* (W. K. Parker, '84), *A*, with most of the membrane bones removed; *B*, membrane bones in place; cartilage stippled. *als*, alisphenoid; *bo*, basioccipital; *bs*, basisphenoid; *c*, condyle; *e*, ethmoid cartilage; *f*, frontal; *g*, mandibular fossa; *m*, maxilla; *oc*, otic capsule; *os*, orbitosphenoid; *pc*, paraseptal cartilage; *pg*, pterygoid; *pl*, palatine; *pm*, premaxilla; *pp*, parotic process; *ps*, presphenoid; *sh*, stylohyoid; *so*, supraoccipital; *sq*, squamosal; *t*, tympanic; *v*, vomer; *z*, zygomatic; V–XII, nerves.

ital surrounds the foramen magnum which is nearly vertical in primitive orders (rodents, bats, some insectivores), but is usually

inclined backwards or may be nearly horizontal. The centre of the basioccipital is the vertebral part of the basal plate and the bone extends forwards into the interotic region. It bears part of the occipital condyle in a few species and occasionally (some whales) is excluded from the foramen magnum. The exoccipitals bear the somewhat oval condyles, their major axes diverging dorsally. In front of each condyle is usually a foramen (**hypoglossal canal**) for the twelfth nerve, but in Monotremes the nerve leaves by the jugular foramen. Usually each exoccipital bears a wing-like **paramastoid** (**paroccipital**) process for muscular attachment on its lateral side
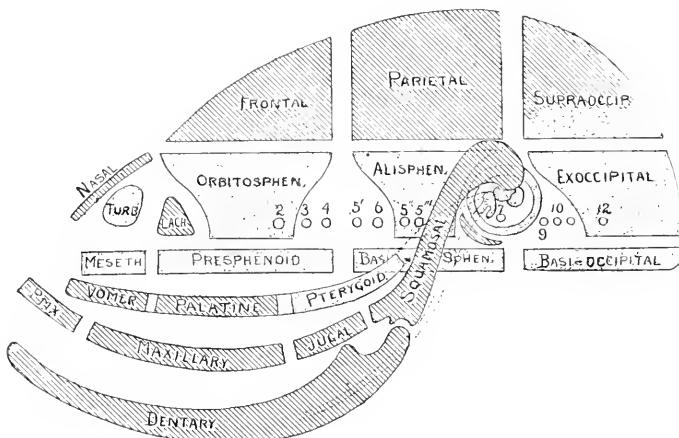
Fig. 200.—Diagram of bones of mammalian skull (altered from Flower). Cartilage bones dotted; membrane bones lined; 2–12, nerve exits.

(fig. 205), this being large in rodents and many Ungulates, etc., reduced or lacking in Primates, whales and Sirenians.

The supraoccipital is the largest of the occipitalia. In lower mammals it ascends obliquely forwards, in Primates backwards and upwards in accordance with the increase in the cerebellum. Usually it is increased in extent in the adult by the union with it of the interparietal.

The sphenoidalia ossify in the basal plate, trabeculæ and ali- and orbitosphenoid cartilages. Both basi- and presphenoid have paired centres of ossification (presphenoid possibly having two pairs). The basisphenoid is usually the larger and bears the sella turcica on its dorsal surface, this being bounded behind by the **dorsum sellæ,** in front by the **sellar tubercle** which separates the two optic foramina

on the line between basi- and presphenoid. In Monotremes and Marsupials the internal carotid artery perforates the basisphenoid; elsewhere it enters the cranium between petrosal and alisphenoid, frequently enclosed in a canal on the former bone. Basisphenoid and basioccipital sometimes fuse, but usually fusion occurs between the basi- and presphenoid, although they are often distinct. The presphenoid (especially prominent in rodents) bears the sulcus for the optic chiasma, and sometimes is excluded from contact with the brain by the meeting of the orbitosphenoids above it. It occasionally fuses with the mesethmoid in front.

The two pairs of sphenoidal wings always fuse with basi- and presphenoid. In Primates the alisphenoid is the larger of the two, but elsewhere the size relations are reversed, rendering inapplicable the terms **ala magna** and **ala parva** of human anatomy. The great width of the brain brings both wings largely to the floor of the cranial cavity, but they also form a part of the side wall and contribute to that of the orbit. Each alisphenoid ossifies from two centres, one for the greater part of the bone, the other in the cartilage inner lamella of the pterygoid process, the outer forming the larger part of the bone. These two lamellæ (with a **pterygoid groove** between them) are strong descending processes from the lower side of the bone, the inner lamella being closely associated with the pterygoid bone of the adult. The relations of alisphenoid to the cranial nerves vary. In many there are foramina ovale and rotundum for the third and second rami of the trigeminal nerve respectively, but ovale and lacerum are continuous in many species, while in most groups rotundum and orbital fissure are not separate.

The orbitosphenoid has a single centre of ossification (fig. 199); it is separated from the alisphenoid by the orbital (sphenoidal) fissure through which, in many mammals, optic, together with the third, fourth, sixth and the ophthalmic ramus of the fifth, nerves pass. But in most higher groups the optic has its own foramen which passes obliquely through the bone, the foramina of the two sides being confluent in some rodents.

The ethmoidalia arise in the septum and lateral walls of the nasal capsule, the olfactory nerves entering the capsule through two foramina in the cartilage separating nasal and cranial cavities. This region (lamina cribrosa) is strongly inclined or nearly vertical in *Ornithorhynchus* and many lower groups, but with increase of the

frontal lobes and consequent overriding of nasal by cranial cavity, it becomes nearly horizontal (elephant, Suids, several Edentates and Primates). Its horizontal position in *Echidna* is due to the large olfactory lobes.

One centre of ossification is in the posterior part of the septum and forms the mesethmoid (perpendicular plate of man). The anterior end of the septum, extending to the tip of the snout, usually persists as cartilage. In pigs and a few other forms a **prenasal (telethmoid) bone** may form in the tip of the nose. There is another centre in each lateral wall, from which ossification extends to the lamina cribrosa, the separate bone thus formed on either side (ectethmoid) soon unites with the hinder part of the mesethmoid, a part of
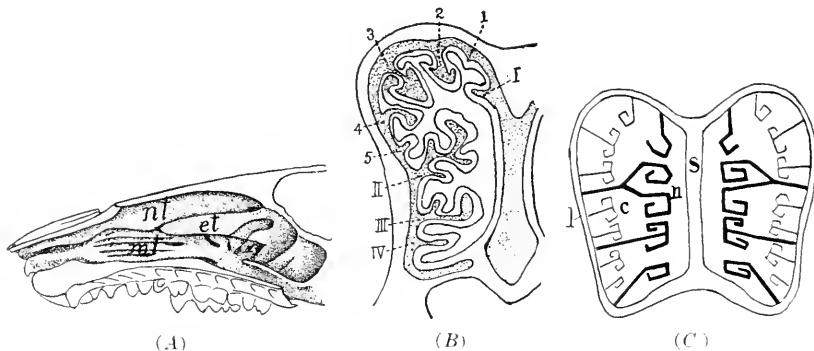
Fig. 201.—Nasal region of mammals; *A*, Nasal cavity of *Erinaceus; B*, section of nasal cavity of new-born dog; *C*, Schema of mammalian turbinals (Paulli). *c*, ectoturbinals; *l*, lateral wall of capsule; *mt*, maxillo-turbinal; *n*, entoturbinals; *nt*, nasoturbinals; *s*, septum; I–IV, entoturbinals; 1–5, entoturbinals; *et*, ethmoturbinal.

which (**crista galli**) may project into the cranial cavity. With the ossification of the cribrosa the primitive olfactory foramina become divided into the several or many openings through which branches of the first nerve pass.

The lateral wall of each capsule extends ventrally to the level of the base of the septum, with which it connects behind, forming the **terminal** (transverse) **lamella,** the lower closure of the olfactory (not respiratory) tract. The ventral wall of each capsule forms the **lamina papyracea,** and its lower margin bends medially, becomes variously complicated, and ossifies separately, forming the **maxillo-turbinal** bone (lower concha, figure 201, *A, B*) which, with a later reduction of the lower lateral wall, becomes attached to the maxilla. Dorsally and farther back each lateral wall bears a series of out-

growths on the medial side, these reaching back to the cribrosa. These ossify as ethmoturbinals, each supporting a part of the olfactory membrane. These conchæ or turbinals constitute the nasal labyrinth, the fibres of the olfactory nerve being distributed to the various folds.

The **ethmoturbinal plates** are usually arranged in two series (fig. 201, C), the **ectoturbinals** which extend farthest towards the septum, and the shorter **entoturbinals** between the first, entoturbinals not developing in *Ornithorhynchus* and being degenerate in Primates. The anterior ethmoturbinal sometimes becomes attached to the nasal bone, and then is a **nasoturbinal.** In a few cases (*Echidna*, Dasypodidæ, *Cholœpus*) other turbinals occur on the perpendicular plate. In general the labyrinth is reduced in vegetable feeders and in Cetacea the olfactory nerve is lost, the cribrosa is imperforate and the labyrinth is gone.

Each nasal cavity begins with a naris at or near the tip of the head (whales excepted, fig. 225; the two nares are united in dolphins). Each naris leads to the nasal cavity, the length of which depends on that of the snout. Each contains the turbinals, largely in the upper (olfactory) part of the chamber, the lower part being the respiratory tract which is continued back of the nasal region as a **naso-pharyngeal duct,** terminating in a choana at the hinder border of vomer and bounded laterally by the descending pterygoid.

In young stages the choanæ are far forwards (fig. 202), about in the same position as in primitive Sauropsida and Amphibia. Then palatal processes of premaxilla, maxilla and palatine extend to the middle line, forming the hard palate which comes between the primitive choanæ and the mouth, so that the former now open into the nasopharyngeal ducts which are bounded below by the hard palate and open behind by the definitive choanæ. The primitive choanæ may be recognized at about the level of the junction

FIG. 202.—Roof of mouth of *Echidna* embryo (Seydel, '99) showing primitive choanæ, *ch*, and palatal folds which meet later cutting off secondary nasal passages from roof of mouth. *et*, egg-tooth; *j*, opening of Jacobson's organ; *pf*, palatal folds.

of the palatal processes of maxillæ and premaxillæ. The nasal cavity also connects with the mouth by one or a pair of **foramina incisiva** (fig. 203, *fi*) in the premaxillary region; these convey nasopalatine canals between the mouth and the organ of Jacobson (vomeronasal organ), the canals being closed in bats,

seals, whales and man (the foramina themselves closed in whales) in all of which Jacobson's organ is rudimentary. When present, the organ is supported or more or less enclosed by the paraseptal cartilage which is connected in front with the septum, behind only in young marsupials.

The nasal cavities may be increased by the formation of cavities (**sinuses**) in the adjacent bones (frontal, maxilla, ethmoid, sphenoid) which are lined by extensions of the olfactory epithelium, their excavation beginning at about the time of ossification. The frontal sinuses are especially developed in elephants, extending through parietals and squamosals nearly to the occipital condyles. The sinuses are large in Ruminants, Perissodactyls and some Marsupials, but are lacking in some Primates, many rodents and Edentates.

The otic capsules, relatively smaller than in other groups, are largely in the cranial floor because of the large brain. Each has from four to six ossification centres, a larger number than is known in other Amniotes and possibly including some of the extra ones of fishes, or two or more centres of mammals may represent one in the lower groups.

One centre is in the dorso-lateral part of the anterior cupula, a second over the inner tip of the cochlea, and a third on the outer posterior end of the capsule, these three usually being regarded as the homologue of the prootic. The epiotic centre is higher on the postero-lateral end, the opisthotic on the ventral side between the fenestra and a sixth centre, more caudal on the medial side. These homologies have not been proved.

These separate centres fuse early to a single **petrosal** (**periotic**) **bone,** articulating with the basioccipital, basisphenoid, exoccipital and alisphenoid. This petrosal bone is firm and hard (whence the name), encloses the labyrinth and has vestibular and cochlear fenestræ in its lateral wall. The foramen lacerum is between it and the alisphenoid, the jugular foramen behind it. These openings and sutures render the petrosal somewhat less firmly attached to the rest of the cranium, and in whales the connexion is so slight that it is readily separated from the rest, forming 'cetoliths.' The **mastoid,** a separate cartilage bone (sometimes absent) lies posterior to the petrosal with which it usually unites, but it never contains any part of the labyrinth. It sometimes has a **paramastoid process** on its lower surface; but when fused with the petrosal, the process is called the **mastoid process.** Its position at the postero-lateral angle of the skull suggests comparison with the parotic or

opisthotic of lower vertebrates. It is vesicular in a few mammals, its cavities being continuous with that of the tympanum.

Membrane Bones.—The interparietal (large in whales, many rodents and some other groups) is known, besides in mammals, only in some Therapsids. It arises from several centres in the membrane between supraoccipital and the parietals, and usually fuses with either the supraoccipital (Perissodactyls, many Carnivores and Primates) or with the parietals (Ruminants, Sirenia, many rodents) or it may persist as one or two independent bones. When parts
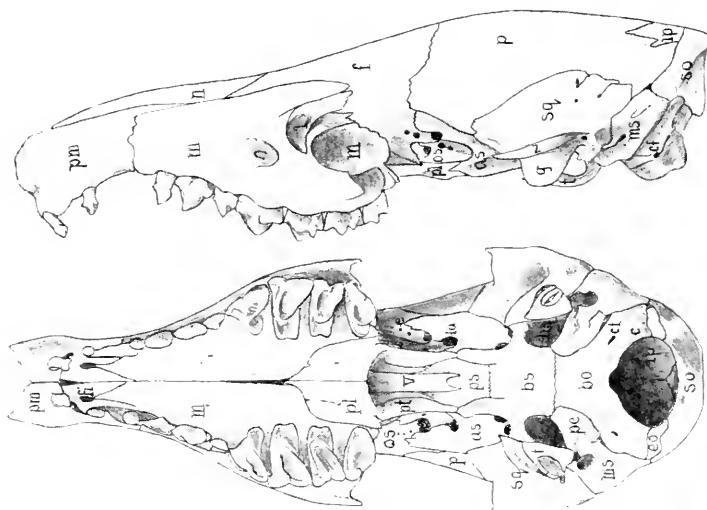
FIG. 203.—Cranium of *Solenodon paradoxus* (Gregory, '10). *as*, alisphenoid; *bo*, basioccipital; *bs*, basisphenoid; *c*, condyle; *cf*, condylar foramen; *e*, supraethmoid foramen; *eo*, exoccipital; *f*, frontal; *fi*, incisive foramen; *g*, glenoid surface; *ip*, interparietal; *l*, lacrimal; *la*, foramen lacerum anterius; *lm*, for. lac. medius; *m*, maxilla; *ms*, mastoid; *n*, nasal; *os*, orbitosphenoid; *p*, parietal; *pe*, petrosal; *pl*, palatine; *pm*, premaxilla; *ps*, presphenoid; *pt*, ?pterygoid; *so*, supraoccipital; *sq*, squamosal; *t*, tympanic; *v*, vomer; *z*, zygomatic.

remain distinct they are the 'Inca bones,' common in the skulls of the former Peruvians. There are frequently small (**sutural** or **Wormian**) **bones,** of no morphological significance, in the lambdoid suture.

The parietals are always large, the pair separated by the sagittal suture or this may be obliterated in the adult (primitive Insectivores, bats, some Ungulates, etc.). An exception to this general rule occurs in whales (fig. 225) where the frontals extend to the supraoccipital, forcing the parietals laterally. *Ornithorhynchus* has a small parietal

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foramen.   Other ossifications may join these paired bones.   Many lower mammals have a fold of membrane (**tentorium**) between cerebrum and cerebellum, which may ossify and join either supraoccipital or parietal, while Monotremes and dolphins have a similar ossification in the membrane (**falx**) between the cerebral hemispheres, this forming a ridge on the under side of the parietals, small in *Echidna*, larger in the duckbill.   Monotremes, some Edentates and Insectivores have a 'pterotic' bone between squamosal and parietal which may exclude the former from the cranial wall.   It develops in some
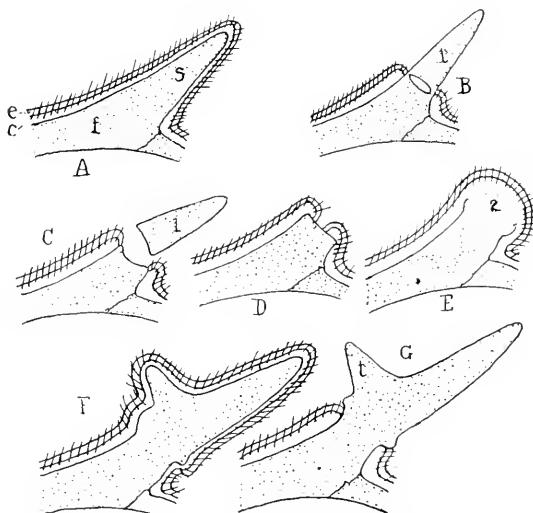
FIG. 204.—History of antler of deer (Nitsche, in Weber, '04). *A*, first appearance of spike as an apophysis of frontal bone; *B*, skin retracted from spike, resorption sinus appears at base of spike; *C*, loss of spike; *D*, *E*, stages in development of antler of second year; covering of pedicel with skin; outgrowth of antler, continued in *F*, with axis and tine shown, the whole covered with skin and hair ('velvet'); *G*, skin retracted from antler.   *c*, corium; *e*, epidermis with hair; *f*, frontal bone; *s*, spike.

other forms, but soon unites with the parietal.   Its position suggests a postfrontal.

The frontals, paired in origin and remaining separate in most mammals (uniting in Monotremes, *Rhinoceros*, *Elephas*, Insectivores and Primates) form the cranial roof between the orbits, meeting the alisphenoids laterally.   Each sends a process into the wall of the orbit and usually a postorbital process which meets the zygomatic, forming the posterior border of the orbit.   As there is a separate centre in this process, it may be postfrontal, a supposition more probable than that pterotic and postfrontal are homologous, since

Ornithorhynchus has a separate bone (*supra*) in the same relative position which later fuses with the orbitosphenoid.

Peculiar to most Ruminants are the **horn-cores** on the frontal bones. In the Cavicornia these are permanent and are covered with epidermal horn. In deer there is a pedicel (fig. 205) on each frontal from which, each year, the antlers grow out and are as regularly shed, the antlers consisting of bone developed from the frontal periosteum, covered at first with skin and hair (velvet) which is soon lost. Similar horn cores occur in the extinct Dinocerata.

The nasal bones which roof the nasal capsules, usually vary in length with that of the snout, but in whales, Proboscidians, Sirenia and a few other forms the nares are far back on the cranium and the nasals are short (nearly vertical in whales, figure 225) and form no part of the nasal roof. The two nasals fuse early in some Old World apes, *Rhinoceros* and some Insectivores; elsewhere the sagittal suture continues between them. The horns of *Rhinoceros*, borne on the nasals, are purely dermal and have no horn core.

The lacrimal lies on the medial (anterior) side of the orbit between frontal and nasal, and usually has both facial and orbital surfaces, but in Primates it is wholly within the orbit. As a rule it is perforated for the lacrimal duct, but not in *Elephas*, peccary and Sirenia, while it is absent as a discrete element in Monotremes, *Manis*, seals and Odontocete whales (possibly fused with other bones). In many Ruminants the facial part is excavated for dermal glands.

The zygomatic bone (lacking in *Echidna*, some Edentates, isolated Insectivores; reduced in *Myrmecophaga*, duckbill and rats) arises below the orbit, of which it forms the lateral and lower wall, and sends a process backwards which usually meets the zygomatic process of the squamosal, forming the zygomatic arch. This arch is incomplete in sloths (fig. 220) in which the connexion is furnished by ligament. Sometimes it has an ascending process which meets the frontal, forming the posterior border of the orbit, separating it externally from the temporal fossa, but there is usually a connexion between the two beneath this postorbital bar, the gap being closed only in Primates where the alisphenoid intervenes.

The squamosal bone ossifies from three centres, one for the upper part (**squama**), one for the zygomatic process, and one in the lower posterior part. The squama is the largest part of the bone, its relative size varying with that of the brain, which, with few

exceptions (where parietal, ali- and orbitosphenoid meet), it aids in enclosing, its participation being small in many Insectivores, bats and some Marsupials. The lower part of the squama has a broad oblique **paramastoid process** extending downwards and inwards to the mastoid, while the **zygomatic process** (enormous in Sirenia and large in many whales) usually meets the zygomatic. On the lower side of the base of the process is the **mandibular** (**glenoid**) **fossa,** a part of which in some mammals is formed by the zygomatic, the alisphenoid contributing in some Marsupials. The form of the fossa, in which the lower jaw is hinged, depends on the motions of the jaw. The fossa is often bounded behind by a postglenoid process which adds to the strength of the articulation.

The zygomatic arch is either the upper arcade of Diapsida or is derived from the single arch of Synapsida by the loss of bones, and in all mammals it has lost the quadratojugal (see, however, p. 182). In some it is nearly straight; others have it stronger and curved outwards, the result of the great development of the chewing muscles, but the arch is incomplete in many Insectivores where the muscles are strong. In Monotremes the arch is composed of maxilla and squamosal, the zygomatic being reduced in *Ornithorhynchus*, absent in *Echidna*.
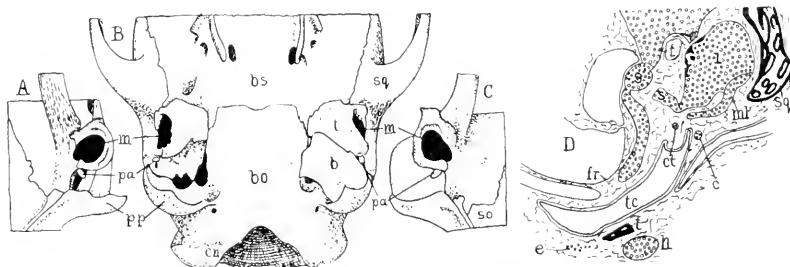
Fig. 205.—*B*, Postero-ventral part of skull of *Paradoxurus; A*, otic region of same with tympanic removed; *C*, side view (Weber, '04); *D*, developing ear region of dog (van der Klaauw, '22). *b*, otic bulla; *bo*, basioccipital; *bs*, basisphenoid; *c*, isolated cartilage; *cn*, condyle; *ct*, chorda tympani; *e*, developing entotympanic; *f*, facial nerve; *h*, hyoid; *i*, incus; *m*, external auditory meatus; *ml*, malleus; *pa*, postauditory process; *pp*, paroccipital process; *s*, stapes; *sq*, squamosal; *t*, tympanic; *tc*, tympanic cavity.

Closely associated with the petrosal is the tympanic bone which begins ossification lateral to the anterior process of the malleus (prearticular part of Meckel's cartilage, figure 212); with growth it gradually curves downwards, below and then behind the auditory meatus, forming a nearly complete ring lateral to the petrosal, a shape retained in Monotremes, Marsupials, Sirenia, most Insectivores and many Primates. In all cases it supports the tympanic membrane and

usually fuses with the petrosal, often also with the squamosal and sometimes with the alisphenoid. At the place where the Meckelian passes from the malleus to the lower jaw, a **petrotympanic (Glaserian) fissure** persists between tympanic and petrosal, this being wide in a few scattered genera. In many mammals (especially Carnivores and Cetacea) the tympanic expands to a vesicle (**tympanic bulla,** fig. 205) surrounding the outer part of the tympanic cavity and auditory meatus, this being supplemented in some genera by an **entotympanic (metatympanic) bone** of cartilage origin, which sometimes retains its individuality.

The tympanic bone arises in the same relation to Meckel's cartilage as does the angulare and seems to be its homologue, but it has lost its connexion with the rest of the lower jaw along with the shifting of the hinge from the quadrate to the squamosal, and, like the quadrate, has become accessory to hearing.

Marsupials have an auditory bulla formed from the alisphenoid. The entotympanic has been recognized in Marsupials, Edentates, Insectivores, Carnivores Ungulates and bats. Where it is apparently lacking it may have fused with other bones.

Premaxillæ, usually bearing thecodont incisor teeth, are always present, but are rudimentary in bats and some Insectivores (correlated with the reduction of the incisors, although well developed in the toothless Mystacocetes). Each has palatal and ascending processes, but a medial ascending process is rare. The bone bounds the naris in front, except in Echidna where it completely surrounds this opening. The premaxillæ of the two sides are usually distinct through life, but in man and Anthropoids they fuse early with the maxillæ. They are very long in whales where the nares are far back on the head. The incisive foramina (p. 191) may be between the palatal processes of the two sides or between them and those of the maxillæ.

Each maxilla arises from several centres which soon unite. Each bone almost always bears thecodont teeth, contributes to both facial and palatal surfaces, and is usually elongate, extremely so in whales where the posterior facial part is expanded and overlaps the frontal in Denticetes, or extends beneath it in Mystacocetes. Its palatal process always meets its fellow in the middle line; it contributes to varying extents to the nasal apparatus, the floor of which is largely formed by the palatal processes, while its medial side adjoins the lateral part of the nasal capsule, and when this is absorbed, the

maxillo-turbinal unites with the maxilla.   There is always an infra-
orbital foramen on the facial part, transmitting a nerve and blood
vessel, but in some rodents this is greatly enlarged, allowing passage
to a part of the masseter muscle.   The bone always forms part of
the floor of the orbit.

The vomer arises from single or paired centres in membrane on
the lower side of the nasal septum, to either side of which it sends a
plate, while ventrally a vertical plate reaches the hard palate.   Its
size varies greatly, being very large in Cetacea, sometimes entering
the cranial wall between sphenoid and ethmoid.   Usually it is hidden
from view from below by the hard palate, though visible through the
choanæ, and in whales between the palatines.   Its possible homology
with the parasphenoid of Ichthyopsida (for which embryological
support is lacking) has been mentioned (p. 77).

Monotremes have a membrane bone, variously called **prevomer, dumb-bell** or
paradoxical bone (fig. 206), the homologies of which are uncertain.   It lies in the
floor of the nasal cavities, medial to the incisive foramina and ventral to the

paraseptal cartilage, and appears in the osseous roof
of the mouth of *Ornithorhynchus*.   In shape it is
somewhat like the body of a violin and has a median
longitudinal crest extending to the nasal septum.   It
arises from paired centres.   It has been suggested
that it is the homologue of the reptilian vomer, and
also that it may be a septomaxillary, a bone found
elsewhere in mammals only in *Tatusia*.

The palatines, in the floor and sides of the
naso-pharyngeal ducts, have horizontal (pala-
tine) and vertical parts, the former, some
whales excepted, forming the hinder part of
the hard palate, the vertical parts forming
the side walls of the ducts and usually entering
the orbits.   In rodents the whole hard palate
is so short that the choanæ are on a level with
the last premolar.

FIG. 206.—Tip of skull of
Echidna (van Bemmeln,
'01). *d*, dumb-bell bone; *mx*,
maxilla; *pm*, premaxilla.

The pterygoid is closely associated with the alisphenoid in the
adult.   The true pterygoid is a membrane bone developing on the
hinder lateral wall of the nasal capsule behind the maxilla.   With this
is more or less closely associated a pterygoid cartilage, sometimes the
median lamella of the alisphenoid, sometimes a separate cartilage.
The bone bounds the postero-lateral part of the naso-pharyngeal

duct, its perpendicular plate lying behind the vertical plate of the palatine and extending to the pterygoid process of the alisphenoid behind. Its inferior end, the **hamulus,** is preformed in cartilage and becomes intimately united with the rest. The pterygoid lacks a palatine process in most mammals, but whales have a strong one, and in *Myrmecophaga* those of the two sides meet in the middle line, carrying the choanæ back nearly to the foramen magnum.

The pterygoid bone is the internal pterygoid process of man. It persists separately in most mammals, although closely connected externally with the pterygoid process of the alisphenoid, often with an **ectopterygoid groove** between them, while a **mesopterygoid fossa** lies between the right and left pterygoids. It is possible that the isolated hamular cartilage or the median lamella of the alisphenoid is the homologue of the pterygoid process of the pterygoquadræ of lower Vertebrates. These parts are widely separated from the quadrate in mammals.

The pterygoid enters the cranial wall in Monotremes, but not elsewhere. This part of the pterygoid, according to Gaupp, is the only homologue of the Saurian pterygoid, the rest of the bone being compared to the posterolateral parts of the parasphenoid. Further study is needed.

The quadrate is considered below in connexion with the ossicula auditus (p. 201). The rest of the mandibular arch (Meckel's cartilage) articulates behind with the incus, the two halves meeting in front. Two bones ossify in either half of this cartilage lower jaw, a mentomeckelian at the anterior end (not known in all mammals) and a **malleus** behind in the articular region, the latter separating from the rest of the Meckelian and becoming one of the bones of the middle ear.

In the adult there is a single bone in either half of the lower jaw, usually called the dentale, the mentomeckelian being absorbed in its front end. The right and left halves meet in front and may be connected by ligament or cartilage, or they may ankylose at the symphysis (Perissodactyls, elephants, bats, toothed whales, apes and man. This dentale terminates behind in a condyle[1] which articulates with the mandibular fossa of the squamosal. In some lower mammals and in those where the muscles are weak, the condylar part is nearly in line with the rest of the bone; elsewhere it is bent at an angle with the rest, forming the ramus of the jaw, the upper posterior part of

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[1] In forms with a mixed diet the condyle is more or less globular, allowing a certain amount of rotation of the lower jaw. Some (especially Carnivores), have it transversely cylindrical (roller), permitting only an up and down motion, while, more rarely it is elongate in the plane of the jaw, allowing only a fore and aft motion.

which bears the condyle and in front of this is a more or less promi-
nent **coronoid process** on which the temporalis muscle is inserted.
When the animal does little chewing (Monotremes, anteaters, mana-
tees, whales, etc.) the process is very small. In many lower
mammals the dentale is extended backwards at an angle where ramus
and body meet, this angle being inflected in Marsupials and some
Insectivores, while in many rodents the strain of the pterygoid muscle
has developed a shelf on the inner side near the angle.

In reality several bones of the lower jaw of the non-mammals may be traced
in the mammals. The true dentale forms in front, mostly on the outer and
inferior sides of the Meckelian, a splenial forming medial to and just above the
cartilage, this forming part of the alveolar border. Some mammals have a large
cartilage lateral to the Meckelian at the angle of the jaw, which has been doubt-
fully compared to the lower labial of fishes. On the upper margin of this carti-
lage is a distinct dermal ossification to which the temporal muscle is attached,
thus corresponding in position and muscular relations to the coronoid bone of
lower forms. The angulare has already been mentioned in connexion with the
tympanic bone; the goniale will be considered in connexion with the malleus
(p. 202).

The hyoid apparatus is largely ossified, both hyoid and first
branchial arches participating (fig. 207), while there is a ligamentary
connexion with the second branchial arch, the
thyreoid cartilage of the larynx. The hyoid
body (basihyal or basibranchial 1?) is occa-
sionally plate-like but is usually a transverse
bar and is sometimes continued forwards as
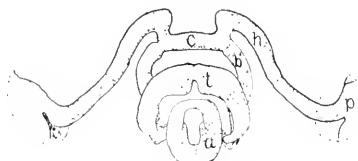
Fig. 207.—Cartilage hyoid apparatus of 27 mm. dog
embryo (Olmstead, '11). *a*, arytenoid; *b*, 1st branchial;
c, hyoid body; *h*, hyoid arch; *p*, parotic crest; *t*, thyreoid
cartilage.
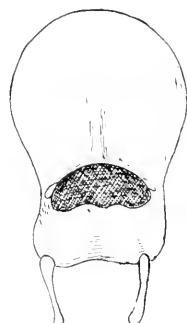
Fig. 208.—Hyoid of
howling monkey, *Mycetes*
(Pouchet et Beauregard,
'89).

a short entoglossal (glossohyal) process. In the howling monkeys
(*Mycetes*, fig. 208) it is expanded and excavate, forming a
resonator for the voice. To the body are attached two pairs of
cornua (visceral arches), the hyoid of man being the **lesser cornu,**
the branchial the **greater,** but in most mammals the hyoid cornu is

the larger. When fully developed the hyoid cornu consists of four elements, usually called, beginning below, **hypo-, cerato-, stylo-** and **tympanohyals,** the dorsal element contributing to the stapes. (It has not been shown that hypo- and ceratohyal are the homologues of the elements with the same name in lower Verte-brates.) The tympanohyal may ankylose with the petrosal, and, fused with the stylohyal, forms the **styloid process.** In other cases the connexion with the stylohyal may be ligamentary, and when, as in man the ceratohyal fails to ossify, a **stylohyal ligament** extends to the hypohyal (lesser cornu). The second horn which is
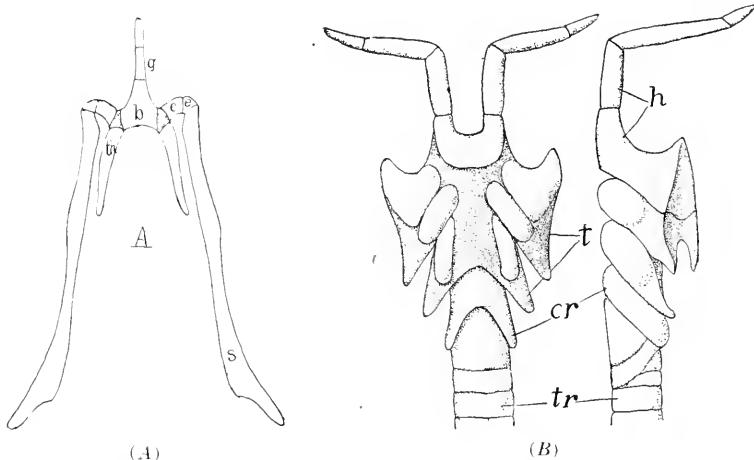
FIG. 209.—A, Hyoid of horse (St. Hilaire); B, ventral and side views of Monotreme larynx (Gegenbaur, '98). b, basihyal; c, ceratohyal; cr, cricoid; e, epihyal; g, glosso-hyal; h, hyoid arch; s, stylohyal; t, thyreoid cartilage; th, thyreohyal; tr, upper part of trachea.

usually coossified with the body, has no connexion with the cranium, but is connected by ligament with the thyreoid cartilage of the larynx. It never contains more than one article.

Ossicula Auditus.—The mammalian ear bones furnish one of the problems around which there is an extensive literature. It has been possible to settle with some degree of certainty the homologies of these elements, but as yet paleontology has not confirmed the con-clusions of comparative anatomy and embryology.

There are three bones in the mammalian middle ear (p. 119) between the fenestra vestibuli (ovale) and the tympanic membrane: a **stapes,** stirrup-shaped and perforated for the stapedial artery, its base lying in the fenestra, while distally it articulates with the second

ossicle of the chain, the **incus.**   This in turn is hinged on the **malleus,** a bone with a body and two processes, a **manubrium** which is attached to the tympanic membrane, and an anterior (**Folian**) **process** extending towards the petro-tympanic fissure.   This chain of bones transmits sound waves across the tympanic cavity from the tympanic membrane to the inner ear through the vestibular fenestra.

In development the malleus arises by ossification of the hinder end of Meckel's cartilage, from which it is later cut off and comes to lie within the tympanum, enveloped in the mucosa of that cavity.   From its body a **manubrium** grows downwards and becomes enveloped in the tympanic membrane, while a short part (Folian process) of the Meckelian extends forwards in the gap between petrosal and tympanic bones.   The articulation of the malleus with the incus is the same in details as that of quadrate and articulare.
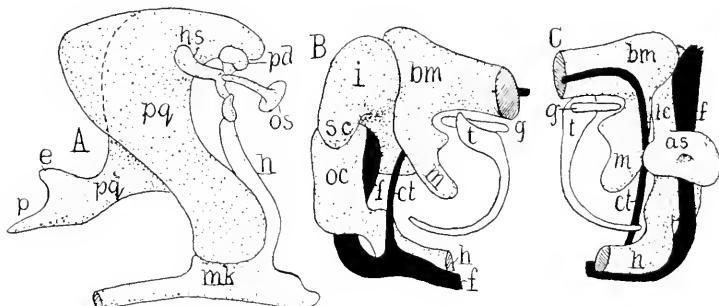
FIG. 210.—Early ossicula auditus and related parts in *A*, *Crocodilus* (Parker, '83) and *B*, *C*, lateral and medial sides of parts in 16 mm. human embryo (Bromann, '99). Nerves black, cartilage stippled, membrane bones white; *as*, stapedial ring; *bm*, body of malleus; *ct*, chorda tympani; *e*, epipterygoid process; *f*, facial nerve; *g*, goniale; *h*, hyoid; *hs*, hyostapes; *i*, incus; *lc*, long crus of incus; *m*, manubrium mallei; *mk*, Meckelian; *oc*, otic capsule; *os*, otostapes; *p*, pterygoid process; *pd*, dorsal process; *pq*, pterygo-quadrate; *sc*, short crus of incus; *t*, tympanic bone.

The incus, in the early stages, articulates with a ridge on the otic capsule, just as does the quadrate of the Sauropsidan, and the resemblance between the two is strengthened by a close connexion of rather dense tissue (fig. 211) between incus and squamosal.   The stapes occupies the same position as in reptiles and unquestionably is the same as at least a part of the reptilian stapes.   In reptiles there is no case known of articulation of quadrate and stapes, but such occurs in Urodeles (p. 119) and Gymnophiona.

The articulare and the proximal part of the reptilian Meckelian are associated closely with two membrane bones, goniale and angulare, the former covering its lower side and extending up on the medial surface, while the angulare is ventral to the goniale and covers the lateral side of the cartilage.   In the developing malleus there are two bones (fig. 212) in exactly the same relative positions. Of these the angulare was homologised above with the tympanic of mammals.

The goniale in reptiles usually fuses with the articulare, and the bone in question in mammals does the same, forming part of the anterior or Folian process.

Another view regards the ossicula auditus of all Amniotes as homologous throughout, the whole columella being equivalent to the three mammalian bones. That this cannot be so is shown by several facts. The columella arises posterior
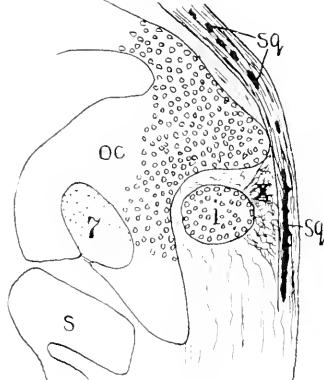
<p style="text-align:center">FIG. 211.   FIG. 212.</p>

FIG. 211.—Relations of incus to otic capsule and developing squamosal in 72 mm. pig (Thyng, '06). *i*, incus; *oc*, part of otic capsule; *s*, stapes; *sq*, squamosal; *x*, dense stroma connecting incus and squamosal.

FIG. 212.—Diagram of ear bones of embryo pig, the tympanic cavity opened. *g*, goniale; *i*, incus; *lj*, part of lower jaw; *m*, malleus; *mk*, Meckel's cartilage; *mm*, manubrium mallei; *s*, stapes; *sq*, squamosal; *z*, zygomatic. Outlines of lower jaw and zygomatic arch dotted.

to the tympanic cavity (part of the spiracular cleft) and invades it from behind; incus and malleus are prespiracular and enter the tympanum from in front. The columellar parts all lie behind the chorda tympani nerve, incus and malleus
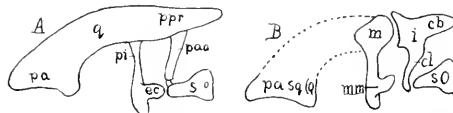
FIG. 213.—Fuchs' ('06) explanation of homologies of Sauropsidan (*A*) and mammalian ossicula auditus (*B*). *cb*, crus brevis; *cl*, crus longus; *ec*, extracolumella; *i*, incus; *m*, body of malleus; *mn*, manubrium; *pa*, articular process of quadrate; *q*, *paa*, accessory anterior process; *pa*, *sq*, *Q*, articular surface of squamosal covered in mandibular fossa by cartilage; *pi*, internal process; *ppr*, preauricular part of quadrate.

(This makes body of malleus a derivative of quadrate—is really a part of Meckelian—and would require transfer of extracolumella, a postotic cartilage, to anterior side of external auditory meatus, etc.).

in front of it. There are other and less probable explanations advanced, one being that mammals have descended from streptostylic reptiles and that the

quadrate has slowly disappeared from the hinge, leaving the lower jaw suspended by the squamosal, a view negatived by the fact that the articulare is always formed from the hinder end of the Meckelian cartilage, while in mammals the Meckelian never approaches the glenoid fossa. It has yet to be proved that the mammals have descended from streptostylic vertebrates, though the close association of squamosal and incus in some species looks that way. Another theory is that the quadrate is the homologue of the tympanic bone, a view which ignores the fact that quadrate is cartilage, the tympanic is dermal in origin.

All theories so far advanced have to meet a serious difficulty for which no explanation has been advanced. That is how the hinge has shifted from the

posterior end of the Meckelian (articulare) and quadrate to the con-dylar squamosal articulation of mam-mals, a shift which must involve a time when there were two hinges to the jaw, both functional at once.

Scarcely anything is known of the skulls of the lowest and oldest orders of mammals, except the teeth and the asso-ciated parts of the jaws. There must have been mammals ear-lier than the upper triassic forms known, of which no traces have been discovered.

MONOTREMATA have skulls prim-itive in some respects, specialized in others. The perforation of the basisphenoid by the internal carotid artery, the identity of optic foramen (also of foramen rotundum in *Ech-idna*), and orbital fissure, the incom-plete tympanic ring and no true tympanic cavity, a separate septo-maxillary in the embryo and the

FIG. 214.— Cranium of *Echidna* (Van Bemmeln, '01). *a*, alisphenoid; *bo*, basiocci-pital; *e*, ethmoid; *bs*, basisphenoid; *f*, frontal; *m*, maxilla; *ms*, mastoid; *p*, parietal; *pf*, postfrontal; *pl*, palatine; *pm*, premaxilla; *pt*, pterygoid; *so*, supraoccipital; *sq*, squamosal.

simple olfactory foramen of *Ornithorhynchus* are primitive or embryonic features; while the absence of most normal sutures, the absence of teeth and the horny sheath of the jaws belong in the second category.

Among other features are the common foramen for nerves IX–XII, the small zygomatic (a small protuberance on the frontal in *Ornithorhynchus*) and its absence in *Echidna*, the zygomatic arch being formed by maxilla and squamosal; and the prevomer in *Ornithorhynchus*. The nares are nearly terminal in *Echidna*, farther back in the duckbill. The occipital condyles of *Echidna* are connected

by cartilage. The choanæ are posterior, the paramastoid process is rudimentary or absent; the lower jaw is reduced and its angle, coronoid process and condyle are little prominent.

MARSUPIALIA have skulls which vary considerably in shape with food and habits, these affecting the teeth more than other parts. The sutures of the cranium largely persist, the four occipitalia often being separate through life. Orbit and temporal fossa are widely connected, often with no sign of postorbital processes. The zygoma is complete, the zygomatic bone extending into the glenoid fossa. The nasals are well developed; there is no separate optic foramen, but the foramen rotundum is present. The lacrimal foramen is in the facial part of the lacrimal bone or just inside the orbit. The semicircular tympanic does not fuse with other bones, it and the alisphenoid forming the tympanic wall, the latter sometimes forming a bulla.
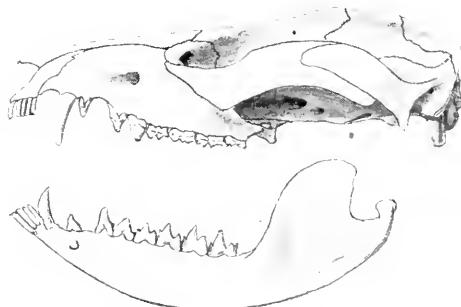
FIG. 215.—Skull of opossum, *Didelphys virginiana*.

There are usually vacuities, sometimes maxillary, sometimes palatine, in the hard palate. The paramastoid process is large in kangaroos, smaller elsewhere. The internal carotid artery pierces the basisphenoid as in Monotremes. The lower jaw, except in *Tarsipes*, has a high coronoid process and an inflected angle. The hyoid body is lozenge-shaped, the ceratohyals broad.

INSECTIVORA.—The skull is usually elongate, especially the facial part, and some genera have the foramen magnum nearly vertical. Cranial sutures are nearly obliterated in Talpids, *Sorex* and some others. Orbit and temporal fossa are usually confluent (*Talpa* and some others excepted), but often a postorbital process from the frontal partially separates them. The facial part of the lacrimal is large, this often containing the foramen. Many genera have optic foramen and orbital fissure united, the foramen rotundum sometimes being included. Ali- and basisphenoid occasionally contribute to the wall of the tympanic cavity and some genera have a tympanic bulla. The petrosal is sometimes only loosely connected with the rest of the cranium. A zygomatic bone is lacking, unless it be fused with the maxilla, which, in *Macroscelides*, extends back to the mandibular fossa. Some (*Erinaceus*, Talpids, etc.) have vacuities in the hard palate, and the vomer in a few genera has broad postero-lateral wings. The halves of the lower jaw are seldom ankylosed, the well-developed angular process is rarely inflected and the condyle is a transverse roller.

CHIROPTERA.—The skulls of bats differ in the two sub-orders, the facial part being long in Macrochiroptera (fig. 217), short in Microchiroptera, the latter having the sutures fused early. The insect-eating Microchiroptera have a sagittal crest for the temporal muscles. Orbit and temporal fossa are usually continuous, but some have a postorbital process of the frontal, and Macrochiroptera have a complete postorbital bar. The foramen magnum is nearly vertical; the broad occipital covers the mastoid. The greater part of the cranial wall is formed by the parietals.

The anterior part of the cranium is most normal in Macrochiroptera where the premaxillæ meet in the median line, as they do in a few Microchiroptera, but most of the latter group have small premaxillæ (sometimes absent) separated by a cleft which may reach the incisive foramen. In these genera the bones are connected by ligaments so that they are moveable, features connected with the reduction of the incisors. The maxillæ often contain large sinuses, expanding the bone externally and giving a strange appearance to the skull and internally reducing the nasal cavities and restricting the conchæ. The lacrimal foramen is in the facial part of the bone. The zygoma is largely maxillary and squamosal, the zygomatic
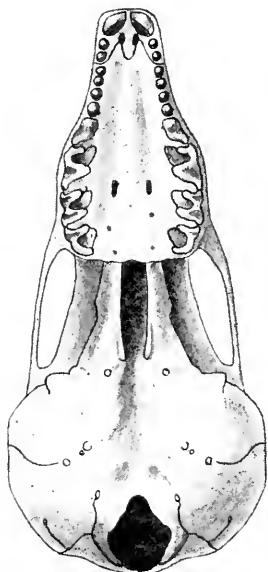
FIG. 216.—Skull of *Scapanus latimanus*.
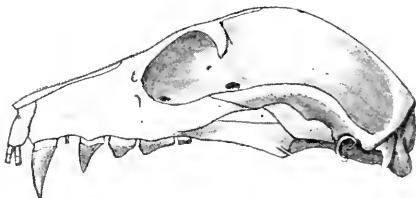
FIG. 217.—Cranium of *Pteropus edwardsii*.

bone being reduced or absent. Orbito- and alisphenoids are only partly ossified and there is no separate optic foramen. The slightly ossified petrosal is loosely connected with the cranium. It is not certain how far the bulla is tympanic or entotympanic. The ramus of the lower jaw is low, the coronoid process strong.

DERMOPTERA.—*Galeopithecus*, the only genus, has a vaulted skull, broad and depressed in front, with a vertical occiput, large orbits, partly separated from the temporal fossæ by postorbital processes of both frontals and zygomatics, the latter bone contributing to the zygomatic arch and extending to the mandibular fossa which is limited behind by a postglenoid process. The lacrimal foramen is within the orbit. A foramen ovale is present, but no f. rotundum. The tympanic bone forms both auditory bulla and external meatus, and the alisphenoid shares in the wall of the tympanic cavity. The condyle of the lower jaw is a transverse roller.

EDENTATA (Bruta).—The old order of Edentates was largely based on dental deficiencies, though most of its members had homodont teeth, from which, except in a few fossils, enamel is lacking. All agree in a cranium rounded above, a sagittal crest being rare, and all, except *Bradyous*, have a separate optic foramen. Recent studies regard the group as polyphyletic and as formed of three separate orders: Tubulidentata (aard vark of Africa); Pholidota (*Manis*, old world anteaters); and Xenarthra (Edentates of America).

TUBULIDENTATA have the facial part of the skull very long; the zygomatic arch complete, the zygomatic bone large; orbit and temporal fossa confluent, there being a slight postorbital process. The occiput is nearly vertical and the supraoccipital just enters the cranial roof, the greater part of which is formed by the parietals. The nasals are long, the nares terminal, while nasals and maxillæ separate the small premaxillæ from the frontals. The lacrimal has a large facial portion which contains the foramen, and the optic foramen is
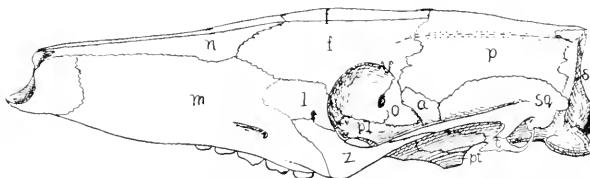
FIG. 218.—Cranium of *Orycteropus* (Weber, '04). *a*, alisphenoid; *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *o*, orbitosphenoid; *p*, parietal; *pl*, palatine; *pt*, pterygoid; *s*, supraoccipital; *sq*, squamosal; *t*, tympanic; *z*, zygomatic.

present. The order is separated from other Edentates by the presence of an interparietal and a tympanohyal. The tympanic bone is open above and is not ankylosed with the adjacent bones. The mandible is slender, highest behind, and has a slender coronoid process and a small oval condyle.

PHOLIDOTA (Effodentia).—The skull is much like that of *Myrmecophaga* (*infra*) both having similar food (ants). It is long conical, rounded dorsally, with orbit and temporal fossa continuous and shallow, and the zygomatic arch is incomplete, the zygomatic bone being but a small remnant on the maxilla. The supraoccipital extends on the cranial roof beyond the limit of the cerebellum, the parietals forming most of the roof. The toothless maxillæ do not meet the frontals. The lacrimal, sometimes fused with the maxilla, is imperforate, the lacrimal duct opening between the frontal and palatine. The squamosal has a large air-filled vesicle above the tympanum, its cavities opening in front and behind. The tympanic forms no part of the osseous meatus. The lower jaw is reduced to a slender bar with condyloid and coronoid processes weaker than in *Echidna*.

XENARTHRA.—The shape of the skull varies, the facial part being long in *Myrmecophaga* (fig. 219), short in other genera, and the cranial cavity is long and narrow. Only armadillos and *Megatherium* have a complete zygoma, it being interrupted in others; but in all the zygomatic bone is large and in sloths has an enormous ventral process (fig. 220). The supraoccipital enters the cranial roof

in *Myrmecophaga*, elsewhere it is included in the vertical occiput. The parietals form much or most of the cranial roof; the nasals are large, the premaxillæ reduced except in a few fossils, and *Megatherium* had one or two prenasal bones between nasals and premaxillæ. Usually the lacrimal is small, the foramen in its facial part. There is no foramen rotundum. The palatal processes of the pterygoids are very large in *Myrmecophaga*, meeting in the middle line and carrying the choanæ back to the level of the auditory meatus, a position paral; leled only in Crocodilia and Cetacea. *Tatusia* has smaller palatal processes-
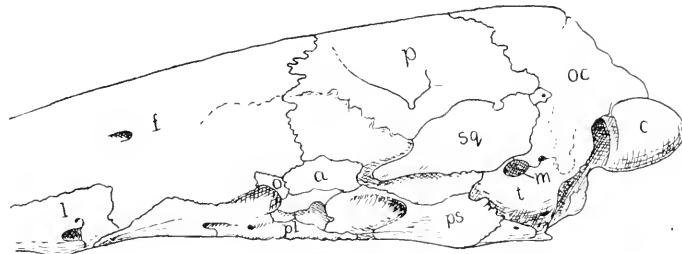
FIG. 219.—Cranium of *Myrmecophaga* (Pouchet in Weber, '04). *a*, alisphenoid; *c*, condyle; *f*, frontal; *l*, lacrimal; *m*, external auditory meatus; *oc*, occipital; *p*, parietal; *pl*, palatine; *ps*, presphenoid; *sq*, squamosal; *t*, tympanic.

they are lacking in other genera. In sloths the posterior end of the pterygoid forms a bulla, connected with the tympanic cavity and with a squamosal cavity, the walls of the cavity being largely membranous. *Dasypus* is noteworthy in having a septomaxillary. The form of the lower jaw varies with the presence or absence of anterior teeth, being respectively U-shaped or V-shaped, with a long symphysis when viewed from above. The ramus is high in *Glyptodon*, moderate in most other genera.
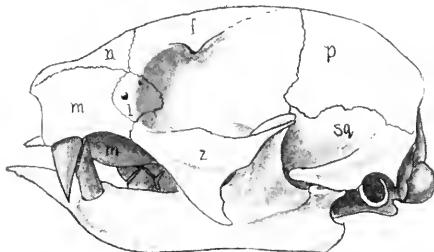
FIG. 220.—Skull of *Cholœpus*. *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *sq*, squamosal; *z*, zygomatic.

RODENTIA (Glires) are characterized more by dentition than by cranial structures. The low skulls have small cranial capacity, a roof largely of frontals, the parietals small; a nearly vertical occiput and foramen magnum, and orbits widely open to the temporal fossæ, there being no postorbital process from the zygomatic arch, and one from the frontal only in squirrels and rabbits. The Zygomatic arch is complete and usually is strong, although its composition varies. In some it is largely maxillary and squamosal, the zygomatic bone being merely

a splint between these (e.g., rats). Other genera have a large zygomatic, forming the lower border of the orbit and even extending to the lacrimal, and sometimes back so that it forms part of the mandibular fossa.

The supraoccipital extends to the roof, and in many Simplicidentata has a lateral process on either side, which may lie on the exoccipital, and sometimes connects with the squamosal. An interparietal is common. The nasals, large and sometimes fused, always over-arch the terminal nares. Each nasal joins the premaxilla, which, because of the large incisors, is large and extends back to the frontal, and has a large diastema on its alveolar margin. A peculiarity of many genera is that a part of the masseter muscle passes through the infraorbital foramen, which is correspondingly enlarged and may unite with the orbit (fig. 221, B). The perforate lacrimal lies within the orbit. The mandibular fossa, which lacks a postglenoid process, permits a fore and aft motion of the lower jaw, but in some the sides of the fossa are elevated, otherwise, as in beaver,
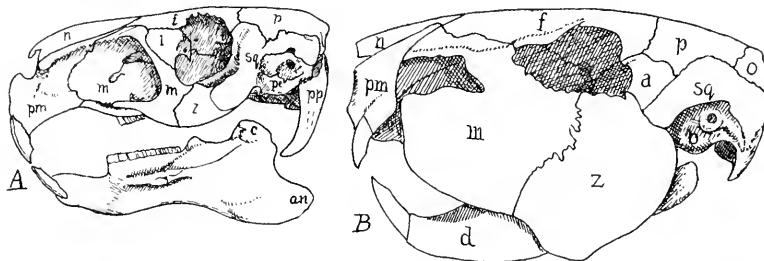
FIG. 221.—A, Skull of *Hydrochœrus capybara* (Zittel, '93); B, of *Cœlogenys paca* (Pouchet et Beauregard, '89). *a*, alisphenoid; *an*, angle of lower jaw; *b*, tympanic bulla; *c*, condyle; *d*, dentale; *f*, frontal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *o*, occipital; *p*, parietal; *pe*, petrosal; *pm*, premaxilla; *pp*, paroccipital process; *sq*, squamosal; *z*, zygomatic.

lateral motion is possible. Some have a separate optic foramen, in others the nerve passes through the orbital fissure. Foramina ovale and rotundum are present except in porcupines and Duplicidentata.

The incisive foramen (sometimes slit-like) is behind the incisors. The hard palate is narrow, and frequently has a deep incision behind, the palatal processes being reduced. The presphenoid is prominent. The petrosal is loosely connected with the other bones, except that the tympanic fuses with it, but not the squamosal. The mastoid, visible between ex- and supraoccipital and squamosal, is often swollen to a vesicle connected with the tympanic cavity, and may reach parietal and interparietal. Posttympanic and paroccipital processes vary. The mandible varies in size and height of its ramus and its coronoid and condyloid processes, and there is always an angular process which encloses a groove on the medial side for the insertion of the pterygoid muscle.

TILLODONTIA are rodent-like in dentition, have low elongate skulls with sagittal crest and low brain capacity. They have a complete zygomatic arch, the zygomatic bone not reaching the mandibular fossa. Orbits and temporal fossa are widely connected; the lacrimal foramen is in the large facial part of the

14

bone. Premaxillæ are large to accommodate the large incisors, the bone extending between the maxillæ to the frontal. The tympanic is small and paroccipital and posttympanic processes are united. There is a postglenoid process in the mandibular fossa; the mandible has a moderate ramus, the coronoid process being higher than the condylar which bears a broad rounded condyle. Both jaws have large diastemata.

CARNIVORA (Feræ) vary in shape of skull, it being either elongate (fig. 222), especially in the facial part, or short and rounded. When long, a sagittal crest is usually well developed, less so in short skulls, the extent of development depending on that of the temporal muscle. The zygomatic arch is well developed and orbit and temporal fossa are connected, but the postorbital processes above and below may be large (actually meeting in the mongoose). Sometimes the occipital condyles extend on the basioccipital, those of the two sides meeting in some Mustelids. The flat occiput is vertical or inclined backwards, parietals and frontals are large, nasals and premaxillaries moderate, the latter not reaching the frontals. The lacrimal in Fissipedia has at most a small facial part; it is greatly reduced in Pinnipedia and lacking in true seals. Separate foramina
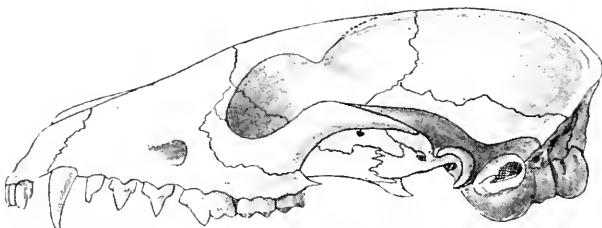
FIG. 222.—Skull of *Urocyon virginianus* (Baird).

opticum, ovale and rotundum occur, except in some seals where the optic nerve runs through the orbital fissure. Some have an alisphenoidal canal. The hard palate ends with the palatines, the choanæ being at or behind the level of the last molar.

The auditory region affords features of systematic use. In Aeluroidea the tympanic bone is more or less annular and forms part of the tympanic wall, the rest being formed by the entotympanic, so that there are two parts to the tympanic cavity, separated (*Hyæna* excepted) by a partition. In Arctoidea the tympanic bone forms the whole outer wall of the cavity (Klaauw recognizes an entotympanic in the dog, figure 205) and a separate centre for the posterior part in others. In Pinnipeds the tympanic bone is flat and thin (Otariidæ) or forms a hard, thick-walled bulla. The paroccipital process varies, sometimes (Arctoids) being separate from the bulla, or may touch or even embrace it. The lower jaw has a strong coronoid process, the roller-like condyle fits in a transverse fossa in the squamosal and the angular process of the lower jaw is small and pointed.

Pinnipedia differ from other Carnivores in the short, round skull with short face and a constriction in the interorbital region. The alisphenoid is not always

distinct. The maxilla has a large infraorbital foramen and the orbital plate of the palatine may be membranous, leaving a gap in the orbit of the dry skull.

CREODONTA (fig. 223) are apparently the parent stock of the Carnivores, and also have Marsupial affinities. They always have a separate optic foramen; usually an alisphenoidal canal occurs, there is a large facial part to the lacrimal, the hard palate is complete and the angle of the lower jaw is not inflected.
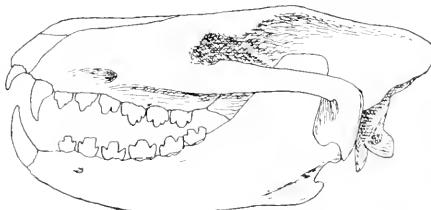
FIG. 223.—Skull of *Mesonyx* (Scott, '86)

CETACEA (Cete).—The three suborders of whales differ considerably in cranial structure. All have spongy bones and the part of the cranium containing the brain never exceeds a quarter of the cranial length. Archicetes and Mysta-cocetes (fig. 224) have a symmetrical cranium, but Odontocetes are more or less asymmetrical, the left premaxilla and maxilla being larger than the right, these features reaching their extreme in *Physeter* and the narwhal. In living species the supraoccipital (with the interparietal) meets the frontals, excluding the
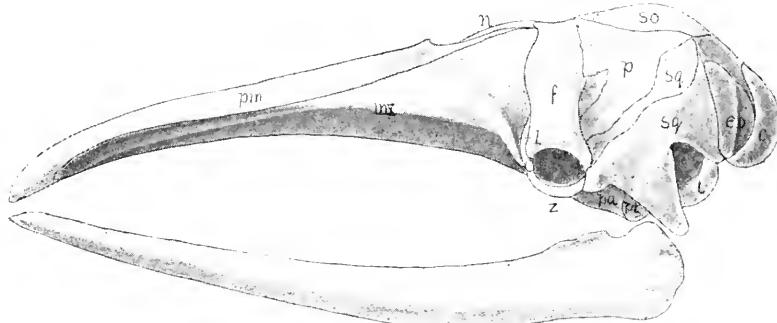
FIG. 224.—Skull of *Balæna japonica* (Boas, in Schimkewitsch). *c*, occipital condyle; *eo*, exoccipital; *f*, frontal; *l*, lacrimal; *mx*, maxilla; *n*, nasal; *p*, parietal; *pa*, palatine; *pm*, premaxilla; *pt*, pterygoid; *so*, supraoccipital; *sq*, squamosal; *t*, tympanic; *z*, zygomatic.

parietals from the middle line, the separation of these being carried so far in Odontocetes (fig. 225) that these bones form no part of the cranial roof, a condition without parallel in other mammals. The relations are more normal in Archicetes. *Zeuglodon* and Mystacocetes have the nares at about the middle of the snout and roofed by long and slender nasals; in Odontocetes the united nares are at the base of the snout, the narial passages are nearly vertical and the

reduced nasals are upright on the hinder side of the opening. The frontals are greatly shortened and extend far laterally, forming a supraorbital plate to which the maxilla contributes in Odontocetes. Since frontals and supraoccipital meet, and with the slight use of the jaws in chewing, there is no sagittal crest in living species, but *Zeuglodon*, with more specialized teeth, has a crest.

In some whales the exoccipitals exclude the basioccipital from the foramen magnum. The maxilla in *Zeuglodon* (fig. 226) is normal, extending back only to the frontal; in Odontocetes it is widened behind, covering much of the supra-orbital plate of the frontal, but in Mystacocetes there is no such over-lapping. The premaxillæ, while long, form only a small part of the border of the mouth in existing whales, much more in *Zeuglodon*. The zygomatic arch is slender, the zygomatic bone lying ventral to the orbit and meeting the imperforate lacrimal; it may fuse with other bones. Occasionally the squamosal meets the postorbital process of the frontal, separating orbit and temporal fossa externally; the orbit being low on the side of the head. The relations of nerves to orbito- and alisphenoid are primitive, the latter being imperforate, and frequently the optic nerve passes through the orbital fissure.

The ethmoid is without olfactory foramina, the nerve being degenerate; the nasal conchæ persist in Mystacocetes, but are degenerate in Odontocetes. Many Mystacocetes have the palatal processes of the pterygoids meeting behind the palatines, carrying the choanæ farther back than in most mammals. The
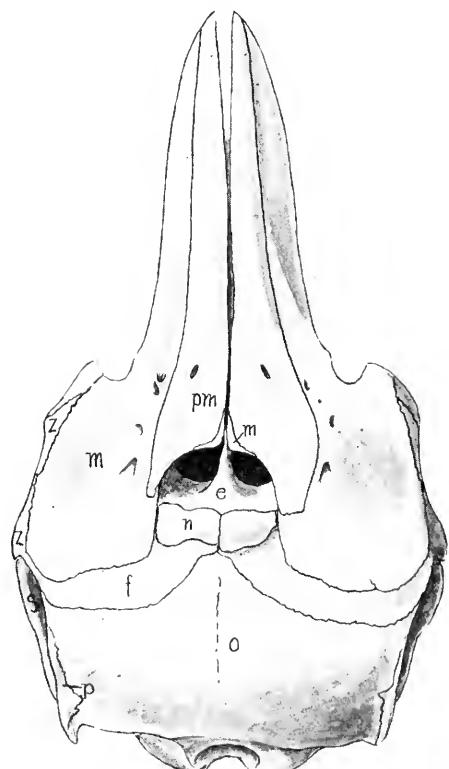
Fig. 225.—Cranium of *Legenorhynchus*. *e*, ethmoid; *f*, facial; *m*, maxilla; *n*, nasal; *o*, occipital; *p*, parietal; *pm*, premaxilla; *s*, squa-mosal; *z*, zygomatic.

petrosal is connected by ligaments to the adjacent bones; it does not project into the cranial cavity, and together with the tympanic with which it is fused, easily separates from the rest of the skull, forming the 'cetoliths' found in deep-sea dredging. The tympanic part forms a very thick bulla. The halves of the lower jaw are cylindrical in Mystacocetes, compressed from side to side in Odontocetes. They are united in front by articulation or ankylosis in Odonto-cetes, merely by ligament in Mystacocetes. In correlation with the slight

development of masticatory muscles the ramus of the lower jaw is low, the coronoid process slight and the condyle rounded.

UNGULATA.—The groups of mammals usually included in an 'order' Ungulata are now regarded as only distantly related to each other and the group as polyphyletic, Artiodactyls and Perissodactyls, being remote from each other, the latter group being more closely related to, among recent forms, the Proboscidia, Hyracoidea and possibly Sirenia. For convenience the older
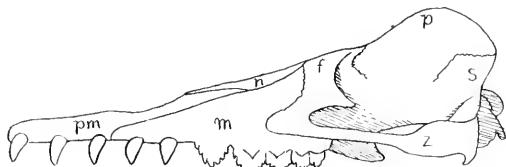
FIG. 226.—Cranium of *Zeuglodon* (von Stromer in Jaekel, '11). *f*, frontal; *m*, maxilla; *n*, nasal; *p*, parietal; *pm*, premaxilla; *s*, squamosal; *z*, zygomatic.

'order' is retained here, although there are few cranial features which are common to all and at the same time distinctive of 'Ungulata.'

The Artiodactyla, a group based on foot structure, have a great variety of skulls. The cranium (largely pneumatic) has a very small brain part; the occipital is nearly vertical or inclined backwards; orbit and temporal fossa may be separated superficially by postorbital processes of frontal and zygomatic, or these may not meet, only partially separating the two spaces. The supraoccipi-
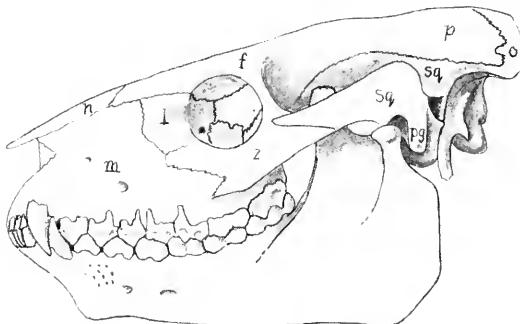
FIG. 227.—Skull of *Oreodon* (Scott, '90). *l*, lacrimal; *m*, maxilla; *n*, nasal; *o*, occipital; *pg*, postglenoid process; *p*, parietal; *sq*, squamosal; *z*, zygomatic.

tal, broadly triangular in Ruminants, usually contains the interparietal, and the parietals are fused in the median line, and in the Cavicornia the common bone thus formed is very small and is forced to the occipital surface by the great development of the frontals; in other groups the parietal is far back on the roof of the cranium. The nasals, usually elongate, are but slightly broadened behind. With the loss of upper incisors the premaxillæ tend towards degeneration. In the pigs they are supplemented by cartilage and prenasal bones in the snout.

The lacrimal bone, perforated by one or more foramina, is variable (small in *Diocotyles*, facial and orbital parts about equal in Ruminants, facial part large in *Hippopotamus*). The maxilla is large to accommodate the large teeth, and in antelopes it is excavate in places for dermal glands. The reduced sphenoid has optic, oval and round foramina, but an alisphenoidal canal is lacking and there is an ectopterygoid fossa except in a few Suids. The squamosal is more of an element in the cranial floor than in most mammals. The hard palate is long, the petrosal small and, as a rule, loosely connected with the rest of the cranium. The tympanic forms a long bulla-like structure, excavate only in Pecora. The mandibular fossa is wholly squamosal and is bounded by a postglenoid ridge or process; its axis is transverse, but permits lateral motion in Ruminants. The lower jaw is all but universally slender, has a high ramus and the halves are united by cartilage at the symphysis.

In non-Ruminants the tympanic fuses with the squamosal, forming a long osseous meatus. Ruminants have a complete postorbital bar. Tylopoda lack horns or antlers on the frontals, these being well developed in at least the males of most Pecora. Both horns and antlers are parts of the skeleton. True horns consist of permanent processes on the frontals (horn cores) covered with horn derived from the skin (mostly epidermal). Antlers are formed annually in the male by outgrowths from the frontal bones (p. 195), these being covered at first by skin and hair ('velvet'). This is soon rubbed off. At yearly intervals the bone of the antler is shed and later replaced as described earlier. Of the true (Cavicorn) horns, the pronghorn of western America differs from all others in the shedding of both horn and core. Giraffes have a tendency towards the formation of a third horn on the nasal bones, this like the other two horns of these animals being covered by skin.

Perissodactyla.—In *Tapirus* and *Rhinoceros*, as in most of the ancestral forms, orbit and temporal fossa are continuous, but in recent Equidæ the orbit is closed behind by a strong process from the frontal to the zygomatic process of the squamosal. Tapirs and horses have a moderate sagittal crest. The interparietal fuses with the parietals; the nasals, expanded behind, are separate except in *Rhinoceros* where they support the horn, (the second horn of *Diceros* is on the frontals), the horns being solely dermal. In tapirs the nasals are short, the nares at about the level of the orbits. The ascending process of the premaxilla extends to the nasals in the Equidæ, bounding the naris laterally; it is shorter in other groups, the maxilla sometimes bounding the naris. The premaxillæ are fused in tapirs, and in all Perissodactyls the palatal processes are small. The maxillæ often extend back beneath the zygoma to accommodate the large molars, and dorsally they enter the floor, but not the margin of the orbit. The facial part of the lacrimal is large in tapirs, the foramen (divided) being in the orbital part.

The alisphenoid usually has an alisphenoidal canal for the maxillary artery, but there is no foramen ovale. The hard palate is largely maxillary, the palatines being small. The mandibular fossa (wholly squamosal) is shallow and short, with a postglenoid process. Tympanic and petrosal are ankylosed, except in tapirs, and are separated from the occipital and sphenoid by a wide cleft which

includes the foramen lacerum in front and the jugular behind the tympano-petrosal. In some rhinoceroses postglenoid and posttympanic processes unite in such a way that an opening, the false auditory meatus, is formed. The mastoid is partly visible in horses, not in others. The lower jaw has a high ramus, the coronoid process is slender, the condyle short, permitting of slight lateral motion. The symphysis of the two halves of the jaw is long in tapirs. The hyoid apparatus (fig. 209) is well ossified and has a long stylohyal connected with the tympanohyal.

Associated with the Perissodactyls are a number of extinct groups as well as the existing Hyracoidea, Proboscidea and Sirenia, which are retained here as separate orders. Of the fossil groups the following deserve mention.

CONDYLARTHRA have skulls recalling Carnivores and Ungulates, and were regarded by Cope as ancestral to the whole group of Ungulates in the wider sense, as well as to other modern forms. The cranium has a small brain case, with a low and long sagittal crest, a slender zygomatic arch; orbits and temporal fossa scarcely separated. The nasals reach back between the orbits, the premaxillæ are weak and the mandibular fossa has a postglenoid process. Both foramen rotundum and alisphenoidal canal are present.

LITOPTERNA.—In some cranial features these fossils resemble the Perisso-dactyls, differ in others. The long cranium with small cavity lacks a crest, the zygomatic arch is complete, the orbit (except in *Thesodon*) is separate from the temporal fossa. The nares are sometimes nearly normal, but in *Macrauchenia* are at about the middle of the dorsal surface, a position which, with the deep pits on the anterior parts of the frontals, suggests the presence of a proboscis some-thing like that of the elephant. The nares, which are vertical as in whales, have large nasals which, except in size, recall those of Sirenia, a resemblance heightened by the frontals. The lacrimal, with from one to three foramina, has a large facial part.

ANCYLOPODA.—This order, largely based on foot structure, falls into three groups, so far as skulls are concerned. The TALIGRADA have non-pneumatic crania, a sagittal crest, premaxillæ extending back to the nasals which lie between the orbits; and are without horns or marked protuberances on the roof. The small orbits are in widest connexion with the temporal fossæ, the coronal suture persists. There is no alisphenoidal canal. The ramus of the lower jaw is high and the condyle faces upwards.

PANTODONTA and DINOCERATA have pneumatic bones, no sagittal crest, the coronal suture is obliterated and there are knobs on the frontals. The Pantodonta have premaxillæ which fall short of the frontals, no protuberances on the maxillæ, rudimentary horns on the parietals; nasals (lacking horns) between the orbits and no alisphenoidal canal. The mandibular ramus is high and the condyle looks obliquely. In Dinocerata nasal and premaxilla meet, small prenasals being present, the nasals short and not reaching the orbits, but bearing horns, while maxillæ and parietals have large horns. An alisphe-noidal canal occurs, the ramus of the lower jaw is low and the condyle faces backwards. All Ancylopda agree in the complete zygomatic, and have at most but a slight postorbital process.

NOTUNGULATA.—*Toxodon*, the best known member, has a vertical occiput, a brain case relatively larger than in recent Ungulates, a strong sagittal crest, nares on the upper side of the snout, the narial passages being roofed by short nasals which hardly extend in front of the posterior ends of the premaxillæ. Orbits and temporal fossæ are confluent, a very strong zygomatic arch occurs and the lacrimal is entirely within the orbit.   *Typotherium* differs in the longer nasals, an occiput inclined backwards and in having a facial part to the lacrimal. *Toxodon* and *Typotherium* have rodent-like incisors.

HYRACOIDEA (fig. 228) have a snout short in relation to the rest of the cranium, a complete zygoma, and orbits far anterior, which are usually separated from the temporal fossæ by postorbital bars, partly frontal, more largely parietal in origin.   There is no sagittal crest, the occiput is nearly vertical and one or two
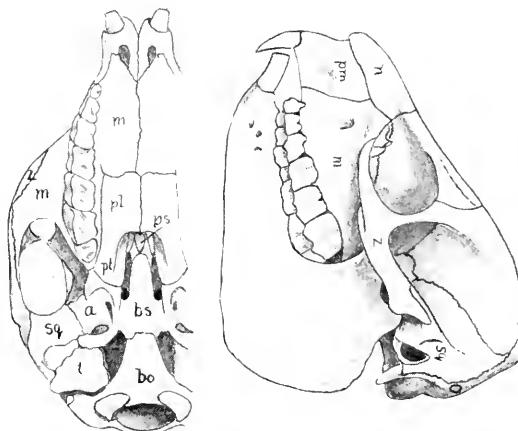
FIG. 228.—Skull of *Procavia capensis* (Weber, '04).   *a*, alisphenoid; *bo*, basioccipital; *bs*, basisphenoid; *m*, maxilla; *n*, nasal; *pl*, palatine; *pm*, premaxilla; *ps*, presphenoid; *pt*, pterygoid; *sq*, squamosal; *t*, tympanic; *z*, zygomatic.

interparietals are present, while the parietals form most of the cranial roof. The broad frontals roof the orbits and meet the broad nasals.   The premaxillæ are short, and the maxillæ (with diastemata) intervene between them and the frontals.   The zygomatic bone forms the lower border of the orbit and extends back to form part of the transverse mandibular fossa.   The perforate lacrimal is small and, lying between maxilla and frontal, extends to the face.   There is an optic foramen, and foramina rotundum and ovale and an alisphenoidal canal perforate the alisphenoid.

The incisive foramina are almost surrounded by the premaxillæ.   The petrosal, with a small mastoid part, is loosely connected with the tympanic. Postglenoid and posttympanic processes are present, the paroccipital process large.   The symphysis of the mandible is low the bone being higher behind. The hyoid is described as differing from that of other mammals in having a transversely oval basal part with which are articulated a pair of flat ceratohyals which

give off in front a pair of long processes which meet in the middle line. Laterally the basihyal is continued in a broad cartilage thyreohyal. Possibly a stylohyal connects with the mastoid.

EMBRYTHOPODA (Barypoda).—The cranium, much like that of Hyracoids in premaxilla, lacrimal, nasal and frontal, has the sutures largely obliterated, a strong lambdoid crest, moderate zygoma, and orbit and temporal fossa continuous. The supraoccipital, excluded from the foramen magnum, inclines forwards, the parietal region is nearly flat, the frontals have small horn cores, larger ones are on the nasals. Lacrimal and nasal are fused, a single incisive foramen occurs, and the orbit is bounded below entirely by the zygomatic bone which extends to the mandibular fossa. The palatines extend laterally far behind the choanæ. There is an alisphenoidal canal. Paroccipital and post-tympanic processes are close together, the latter bounding the auditory meatus behind. Pre- and postglenoid processes are present. The halves of the lower jaw are fused in a long symphysis, the coronoid process is high, the condylar, with a rounded condyle, is slight.

PROBOSCIDIA.—The skulls of elephants and their allies are larger because of extensive pneumatization, there being numerous spaces in the cranial walls (fig. 229), the cavities extending into several of the facial bones. The history of the order, now pretty well known, shows an increase in skull size to accommodate the incisors (tusks) and molars which are very large in recent species. This increase is seen especially in the premaxillæ, the great size of which and the development of the trunk, carries the nares back so that the nasal canals and the mesethmoid are nearly vertical, the nasal bones being reduced. Except in *Dinotherium*, orbit and temporal fossa

FIG. 229.—Section of cranium of elephant (Zittel, '93). *b*, brain-case; *c*, condyle; *e*, ethmoid; *f*, frontal; *i*, incisor (tusk); *m*, maxilla; *n*, naris; *p*, parietal; *pm*, premaxilla; *s*, supraoccipital; 1, 2, molars.

are partly separated by postorbital processes. The zygoma is slender, the zygomatic bone forming its middle part.

The supraoccipital separates the parietals behind, it and the parietals forming most of the roof of the cranial cavity, the latter reaching down in the side walls to the squamosals, these parts separating squamosals and supraoccipital. The frontals roof the orbits; the lacrimal, perforate or entire, is small and sometimes is fused with the adjacent bones. Tympanic and petrosal fuse early, both forming the bulla. A postglenoid process is absent, and the posttympanic limits the circular mandibular fossa behind and encloses the auditory meatus. The halves of the lower jaw are fused at the symphysis, the ramus is high, the condyle rounded and the alveolar part of the jaw is large. The condylar process is usually lower than the coronoid.

The oldest Proboscidians (*Mærotherium* and *Palæomastodon*, had incisors in both jaws. From these two lines developed. *Dinotherium* lacks the upper incisors, the lower turned downwards. True elephants have lost the lower incisors, the upper forming the tusks which reached their extreme in the mammoths.

SIRENIA.—Although often placed near the whales, the manatees differ widely from them in crania and are more like the Ungulates. The cranial cavity is cylindrical, the foramen magnum large and the zygoma complete, largely formed by the process of the squamosal, the zygomatic bone forming most of the floor of the large orbit, which is separated in part from the temporal fossa by post-orbital processes of frontal and zygomatic, the separation being most nearly complete in *Manatus senegalensis* (fig. 230). The four occipitalia are separate,
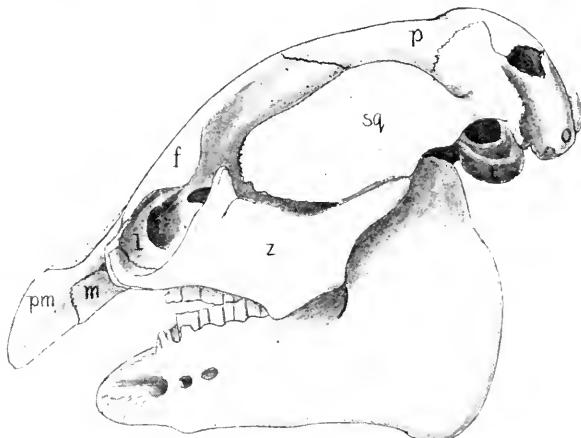
FIG. 230.—Skull of *Manatus senegalensis*. *f*, frontal; *m*, maxilla; *o*, occipital; *p*, parietal; *pm*, premaxilla; *t*, tympanic; *z*, zygomatic.

the supraoccipital extending forwards into the angle between the fused parietals. The nares are dorsal and the nasals (lacking in *Halicore*) are small; the greatly elongate premaxillæ diverge behind, form the lateral borders of the nares and reach the frontals (in some fossils the nasals cover part of the nasal passages). The short maxilla joins the zygomatic by a lateral process, its palatal processs forming much of the hard palate. The small, often imperforate, lacrimal is absent in some.

The alisphenoid is without foramina, the lower rami of nerve V passing out through the foramen lacerum; the optic foramen is a long tube in the orbito-sphenoid. The tympanic (a half ring in *Halicore*, nearly complete in *Manatus*) is partly fused with the petrosal, between which and the occipitals and squamosal is a gap, largest in *Halicore*. The palatine part of the hard palate is short. The incisive foramen, between maxilla, and premaxilla, leads to a long tube which passes back to the nares. The lower jaw has a long symphysis, a rather high and small coronoid process and a large, nearly flat condyle.

PRIMATES (sens. lat.).—The primate skull has a wide range of form from the lowest Lemuroid to man. The facial parts in the lowest genera recall those of Carnivores, and the brain cavity is as small relatively as in that group. In the highest genera the increase in size of the brain increases the posterior part of the skull so that the face is less prominent. All Primates have an complete zygoma and the orbit is separated from the temporal fossa by a postorbital bar, the separation being so complete in apes and man that only a narrow cleft remains between bar and the rest of the cranium. The orbits themselves are directed more or less forwards. Some genera have a sagittal crest, others have none. The position of the occiput also varies, being nearly vertical in the lower, nearly horizontal in the higher groups, there being a few exceptions to both statements. Ali- and orbitosphenoids fuse with basi- and presphenoid respectively, forming the alæ magnæ and parvæ of human anatomy; and often fusion of basi- and presphenoids results in a single sphenoid bone.

Prosimiæ (Lemuroidea) usually have the facial part of the cranium elongate, a sagittal crest of varying size, and frequently an interparietal. The orbit is
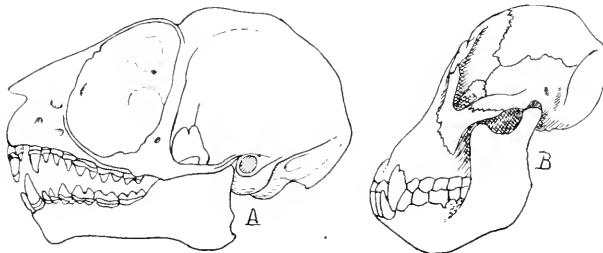
FIG. 231.—Skulls of (A) *Tarsius* (Gregory, '20), and (B) adult orang-utan (Wiedersheim, '08).

largely bounded by zygomatic and frontal, lacrimal and ethmoid being less prominent. The orbit is connected with the temporal fossa beneath the post-orbital bar. The zygomatic arch is usually slender, the zygomatic bone not reaching the shallow mandibular fossa which often has a postglenoid process. The lacrimal foramen may be in the bone or between it and the maxilla. The alisphenoid reaches the frontal and lacks a foramen rotundum. An optic foramen is present. The small premaxillæ reach the nasals. The hard palate is long. The halves of the lower jaw are rarely fused at the symphysis, the ramus is high and the condyle rounded.

Tarsius (fig. 231, A) needs special mention, since, while Lemurine in general make-up, it is like man in many cranial features and consequently has received much attention. Among these points are the short facial region, the small cleft beneath the postocular bar, no sagittal crest, and enormous orbits. *Tarsius* is one of the very few mammals with a single olfactory foramen on either side of the ethmoid.

Primates sens. str.).—In Primates the brain overhangs the nasal region so that the cribrosa is horizontal, while the extension of the brain backwards results

in an occiput, either strongly inclined backwards or even all but horizontal. In the young the cranium is rounded, permanently so in man, but other genera tend towards a prognathism in the adult and a consequent elongation of the skull. A sagittal crest is common (except in American monkeys), especially so in Anthropomorphæ (fig. 231, *B*), and the old world species often have a strong supraorbital crest. All Primates have pneumatic bones. The orbits are directed forwards and almost completely separated from the temporal fossæ. Their position results in a narrowing of the posterior part of the nasal cavities and reduction of the conchæ. The lateral wall of the orbit in American species is largely formed by the zygomatic bone; in old world genera more by alisphenoid and frontal. In all, the ethmoid enters its median wall and the lacrimal bone and its foramen are within the orbit. Fusion of the frontals is common and the nasals may ankylose. The latter bones and the premaxillæ usually bound the nares; the premaxillæ fuse early with the maxillæ.

The alisphenoid has a large pterygoid process, separated from the true pterygoid by an entopterygoid fossa of varying width, and is pierced by the foramen rotundum. It is stated that young apes have a thin interorbital septum; whether this be an inheritance from some tropibasic ancestor or a new acquisition is not decided. Petrosal and mastoid fuse; the tympanic is annular, walling the external meatus and usually fusing with the petrosal and squamosal, forming the temporal bone. The shallow mandibular fossa has a postglenoid process. The halves of the lower jaw are fused, the ramus high, its angle rounded, the coronoid process well developed and the condyle is broadly transverse.

APPENDICULAR SKELETON

Vertebrates may have two kinds of appendages, median (azygos or unpaired) and paired. The discussion of their origin (p. 241) best follows the account of the structure of both. Both are integumental folds into which mesenchyme and usually mesothelial muscles extend. Development shows that both kinds are markedly metameric at first, the repetition of parts affecting not only the primitive musculature, but nerves, blood vessels and skeletal parts as well.

In their simplest form the skeletal parts of the appendages consist of a series of parallel cartilage rods or rays, to which, in fishes are added more distal parts (**actinotrichia**), horny in character, which are not metameric, but are paired in origin and more numerous than the somites entering the appendage. Primitively each cartilage ray is divided into a **basale,** either enveloped in the body or close to it, and one or more **radialia** which extend into the free appendage. In most Vertebrates these parts are considerably modified, least so in the median appendages.

Actinotrichia differ in Elasmobranchs and other fishes. In the former they are horny and non-cellular, and resemble elastic-tissue fibres (**ceratotrichia**). In Teleosts, Ganoids and Dipnoi they contain bone cells and are called **lepido-trichia,** and may, to varying extents, be converted into bone, or may be enclosed in bone of dermal origin.

MEDIAN (Azygos) APPENDAGES

Although median appendages appear here and there in higher classes (aquatic Urodeles, larval Anura, Crocodilia, dorsal crests of some lizards and dorsal fins of Ichthyosaurs and whales), they have an internal skeleton only in Cyclostomes and Fishes, apart from the spinous processes of the vertebræ. Hence all except these two divisions may be dismissed without further mention. Before describing the skeleton of the median fins, a word is necessary concerning their modifications.

The median fins (**pinnæ**) are primitively derived from a continuous median fold, beginning on the back, just behind the head,
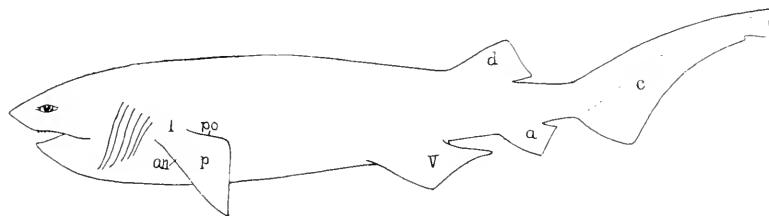
FIG. 232.—*Hexanchus griseus* (Jordan and Evermann, '00). *a*, anal; *c*, caudal; *d*, dorsal; *p*, pectoral and *v*, ventral fins. *an* and *po*, anterior and posterior borders of fin; *l*, nearly horizontal line of attachment to trunk; the side of the pectoral fin shown is dorsal side.

extending around the tip of the tail and passing forwards on the ventral surface as far as the anus. The posterior part of this fold (**caudal fin**) is most strongly developed and is usually the principal locomotor organ, the other parts of the fold acting more as keels. From this continuous fold all median fins are derived by overgrowth (hypertrophy) of parts and obsolescence or complete disappearance of others. With this formation of gaps one or more **dorsal fins** (fig. 232) are differentiated from the caudal fin, which, in turn, is similarly separated from an **anal fin,** on the ventral side just behind the anus. The caudal excepted, any of these fins may disappear, and the caudal may be greatly reduced as in skates and some

Teleosts.   The dorsal fin is frequently divided into two or more parts, while the anal is rarely interrupted, though sometimes absent.

The caudal fin undergoes the most modifications (fig. 233).   In what must be regarded as the primitive condition, the vertebral axis extends in a straight line through the tail, and the caudal fin is arranged symmetrically about it (**diphycercal tail**).   This is the earliest stage in all fishes and it persists in Cyclostomes, Dipnoi and some Teleosts.   In all others this stage is followed by a **heterocercal** tail in which the vertebral axis is bent upwards, while the anterior part of the ventral fold (**hypochordal lobe**) is greatly enlarged, so that the whole fin appears as if composed of two unequal lobes, the vertebral axis extending into the upper of these.   *Amia* (Ganoid) and
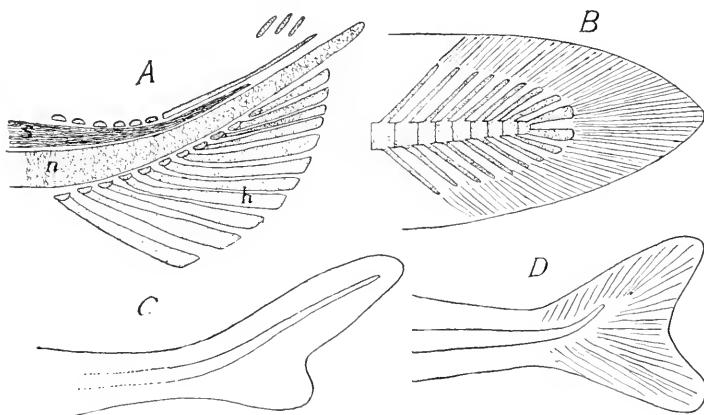
FIG. 233.—Tails of fishes.   *A*, young *Amia*; *B*, diphycercal; *C*, heterocercal; *D* homocercal; *h*, hypurals; *n*, notochord; *s*, spinal cord.

Teleosts pass through this heterocercal condition which is permanent in other Ganoids and in Elasmobranchs, and then have a greater development of the hypochordal lobe, the result being that the upper and lower lobes appear equal (**homocercal**) although internally they retain the bent vertebral axis.   The homocercal tail may be rounded or excavate at the end.

As implied above, *Amia* agrees with most Teleosts in being homocercal. *Polypterus*, many eels and a few other Teleosts are diphycercal, probably a retrograde condition.

Caudal fins are developed in a few other Vertebrates.   Ichthyosaurs have a heterocercal tail, but here the vertebral column extends into the ventral lobe of the tail.   In Cetacea and Sirenia the tail bears horizontal rather than vertical

lobes ('flukes'). All of these are without skeletal supports other than the vertebræ.

CYCLOSTOMATA.—These eel-like animals have the median fins continuous, there being but slight differentiation of caudal, dorsal and anal regions. The skeleton of the fin proper consists of filiform cartilage rods, irregularly arranged (up to four to a somite in *Petromyzon*), each split distally in a dichotomous manner. Anteriorly these rods are not connected with the reduced axial skeleton, but in the tail their bases are fused and the resulting plates are either articulated (*Petromyzon*) or fused with the united neural and hæmal arches (Myxinoids, figure 234). These rods show no traces of division into basal and radial parts as do those of true fishes.

FIG. 234.—Caudal region of *Myxine* (Cole, '05). *d*, dorsal cartilage; *f*, fin rays; *n*, notochord; *s*, spinal cord; *v*, ventral cartilage.

FISHES have the skeleton of the median fins partly cartilage, partly dermal in origin. In the simplest condition of dorsal and anal fins the cartilage parts consist of a series of rods, often more numerous than the vertebræ, which are partly or wholly embedded between the trunk muscles of the two sides of the body. These rods have various names, **pterygophores** possibly being the best. In Elasmobranchs each pterygophore is usually divided into a deeper **basal** and a more superficial **radial,** the radial often being subdivided, the distal segment then being a **marginal.** These pterygophores support the actinotrichia which arise in the skin on either side of the fin, their proximal ends embracing the distal ends of the pterygophores.

In Elasmobranchs the pterygophores remain cartilage; in Teleostomes (*Acipenser* and a few others excepted) they are ossified, there usually being two (sometimes three) elements in each, the one or two basal being called **axinosts** or **interspinals,** the distal being a **baseost.** The number of axinosts and baseosts usually corresponds to that of the vertebræ at either end of the fin, but in the middle they may be more numerous, even up to four to a somite. In Elasmobranchs the basalia often fuse to large plates (fig. 238) and less frequently there is a similar fusion of radial parts. The pterygophores often extend over more somites than does the fin itself, possibly the result of reduction of the continuous fin. Only the

basalia in Elasmobranchs are included in the body, the radialia being largely in the fin. In Teleosts the axinosts are wholly within the trunk, the baseosts reaching the surface. At either end of the fin the axinosts alternate (sometimes articulate) with the spinous processes of the vertebræ, while the baseosts usually articulate with two adjacent axinosts.

In Elasmobranchs there is no close connexion of actinotrichia with radials, their basal ends lying in the tissue on either side of the radialia. In Teleostomes, where the ceratotrichia of Elasmo-branchs are replaced by lepidotrichia (p. 221), the skeleton of the
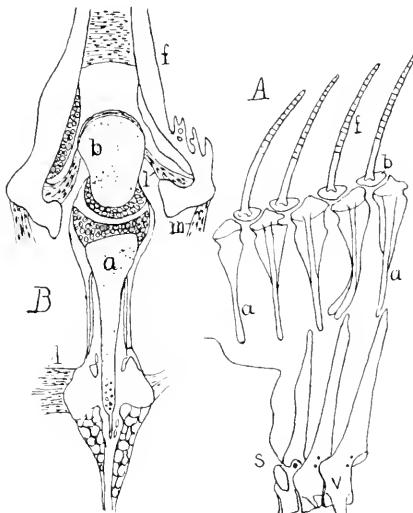
Fig. 235.—Skeleton of dorsal fin of *Pleuronectes* (Cole and Johnstone, '01). *A*, just behind head; *B*, section. *a*, actinost; *b*, baseost; *f*, fin rays; *l*, ligament; *m*, muscle; *s*, base of skull; *v*, vertebræ.

free fin (arising as paired structures which fuse) embraces the baseosts (fig. 235, *B*). The ceratotrichia are not divided transversely. The lepidotrichia are more or less ossified and present two conditions. Where fully ossified (almost always at the anterior end of dorsal and anal fins) they are strong unsegmented spines (spinous rays of ichthyology). With less lime they are 'soft rays,' usually divided transversely into small articles. Distally the soft rays may branch several times.

The median fins of Malacopterygii, most Physostomes, Plectognaths and Anacanthini are supported wholly by soft rays. Acanthopterygii have both spinous and soft rays in dorsal and anal fins.

The caudal fins (diphycercal excepted) differ from dorsal and anal in the apparent absence of pterygophores, the actinotrichia being supported on the spinous processes of the vertebræ. Both arches, neural and hæmal are about equally developed in the diphycercal tail, diminishing in size towards the tip, the actinotrichia
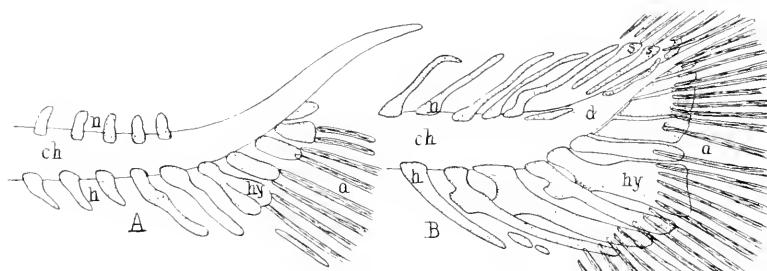
FIG. 236.—Developing caudal skeleton of *Salmo* (Schmalhausen, '12). *A*, 16 mm. larva; *B*, 19 mm. larva. *a*, actinotrichia; *ch*, notochord; *d*, *n*, neural arches; *h*, hæmal arches; *hy*, hypurals; *s*, spinous process.

being supported on elements radial in character. The upward bend of the vertebral column in heterocercal caudals results in the reduction of the neural arches and hypertrophy of the hæmals. The same conditions persist in the (homocercal) Teleosts the hæmals being greatly expanded) (figs. 236, 237), forming **hypural bones,** often fused
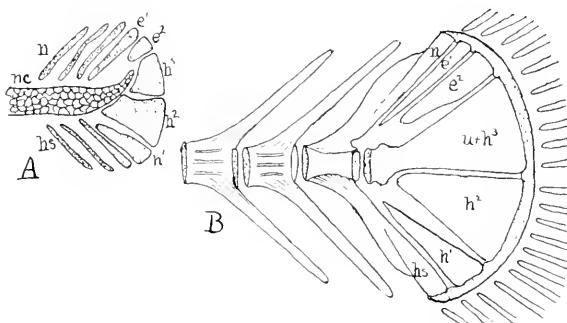
FIG. 237.—Skeleton of caudal fin of *Pleuronectes* (Cole and Johnstone '01). *A*, 17 mm. larva; *B*, adult; *e*, epurals; *h*, hypurals; *hs*, hæmal spines; *n*, neural spines; *nc*, notochord; *u + h*, fused 3d hypural and urostyle.

to large plates. In Teleosts no separate centra form in the tip of the caudal fin, but a rod-like sheath of bone, the **urostyle,** more or less completely surrounds the end of the notochord. Eels have the hypurals reduced, the urostyle short and the lobe of the fin extended

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forwards so that the skeleton appears symmetrical, a secondary diphycercy.

Some Elasmobranchs (Spinacids, Cestracionids, some Holocephals) have a large spine in front of the dorsal fin (fig. 238). This is a modified dermal scale supported on the anterior side of a pterygophore. The spine exists independent
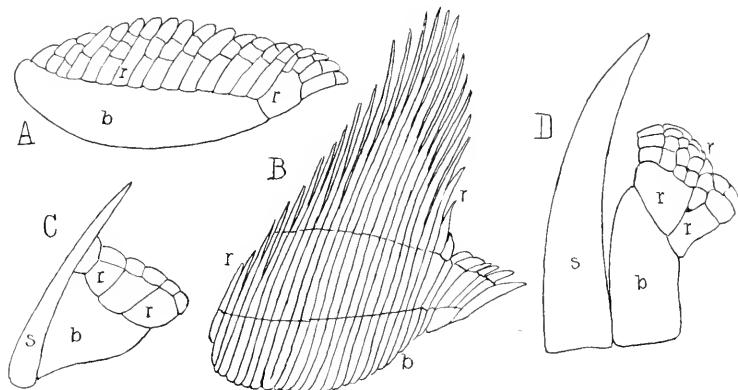
FIG. 238.—Skeletons of dorsal fins of (A) *Heptanchus*, (B) *Zygæna*, (C) *Acanthias* (Mivart, '79); (D), *Heterodontus* (Daniel, '15). *b*, basalia; *r*, radialia; *s*, spine.

of a fin on the tail of sting rays. The Elasmobranch pterygophores arise from a continuous procartilage, the separate rays appearing on chondrification. The radials are often shortened to polygonal plates (fig. 238, *D*).

Characteristic of most Ganoids are **fulcra**, two rows of overlapping modified scales (those of the two sides usually united to an inverted V) on the anterior margin of the median fins. *Acipenser* has the caudal fin supported on cartilage rods (either radials or separate spinous processes). The dorsal fin of *Polypterus*, continuous in the embryo, is divided into a number of finlets (fig. 240), each with an anterior spine (modified scale) supported on an axinost and bearing a series of lepidotrichia on its posterior border.

FIG. 239.— Two finlets of *Polypterus* (Goodrich, '09). *a*, actinost; *l*, lepidotrichia supporting fin-membrane; *s*, spine of finlet.

In Teleosts, where the rays are mostly lepidotrichia, remnants of ceratitrichia persist at least for a time, between the lepidotrichia of the two sides and also in the adipose fin of Salmonids.

The sucker of remoras is a peculiar flattened fin in which the axinosts are transverse bars with lepidotrichia between them.

PAIRED APPENDAGES

The limbless Cyclostomes excepted, most members of every class of Vertebrates have typically two pairs of appendages (fig. 232), an anterior (**pectoral**) pair, arising primitively just behind the last gill-cleft; and a posterior (**pelvic** or **ventral**) pair just in front of the anus. A few genera of all classes may lack one or both pairs, while the position may vary in members of the different groups.

The most primitive condition of the paired appendages occurs in fishes, those of Tetrapoda being very different. Fishes have paired fins (**pterygia**), paddle-like appendages; Tetrapoda have jointed legs (**podia**). Pterygia are the more primitive, and from them podia have undoubtedly arisen, although the steps in this evolution are far from evident. Both arise, ontogenetically, as longitudinal folds
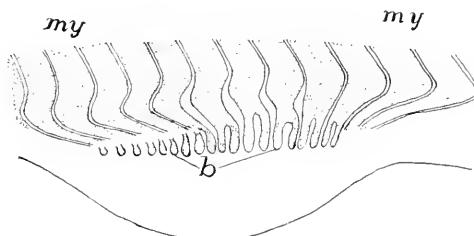
Fig. 240.—Budding of appendicular muscles from myotomes in *Pristiurus* (Rabl). *b*, muscle buds; *my*, myotomes.

extending over several somites in the lateral trunk region (fig. 240), the number of somites concerned frequently being greater than that entering the definitive appendage, the extreme number being reached in the pectoral fin of skates. Each fold is a duplicature of ectoderm, carried out by increase in the underlying mesoderm, the fold containing muscle-buds, nerves, blood vessels and scleroblasts.

At first the fin folds are horizontal with dorsal and ventral surfaces, anterior (**preaxial**) and posterior (**postaxial**) borders, relations persisting in the pectoral fins of adult skates. Elsewhere the anterior border of each fin grows faster than the posterior so that the fin becomes triangular or trapezoidal. Also, in most fishes, and easiest recognized in the pectorals, the line of attachment of fin to trunk shifts so that the anterior border is moved upwards and the original ventral surface is turned towards the front. This may go so far with the pectoral fin that the line of attachment to the body becomes vertical and the dorsal side of the fin is turned towards the

body when at rest. There is less shifting or torsion in the pelvic fin, but here the fins are so placed that the preaxial border is lateral, the postaxial turned towards the body.

Except in a few primitive Gnathostomes, the skeleton of the limbs (always laid down in cartilage) becomes differentiated into a support (**girdle**) enclosed in the trunk, and the skeleton of the free append-age. Thus there are two girdles, **pectoral** (shoulder) and **pelvic,** and fore and hind limbs (either pterygia or podia) according to their position.

The pectoral girdle is always near the heart, be that organ near the gill-clefts or much farther back. Normally the pelvic girdle is near the anus and thus remote from the anterior limbs, but in some Teleosts the pelvic fins may move forwards to a point nearly between the pectoral fins (the old group of 'Thora-cici'), or even in front of them ('Jugulares').

GIRDLES

The typical girdle (fig. 241) is an inverted arch in the somatic wall of the trunk, extending across the mid-ventral line and upwards

FIG. 241.—Pectoral girdle and fin-skeletons of *Scyllium*. *c*, coracoid region; *g*, glenoid surface; *ms*, mesop-terygium; *mt*, metapterygium; *p*, pro-pterygium; *r*, radialia; *s*, scapular region.

on either side of the body. The pectoral girdle is frequently con-nected with the axial skeleton (skull or vertebral column) in fishes, but not in Tetrapoda. The pelvic girdle reverses these relations, being free in fishes, while in Tetrapoda, where the hind limbs bear much of the body weight, the pelvic girdle is attached to one or more **sacral vertebræ.**

The skeleton of the free append-age is articulated to the corre-sponding side of the girdle, the point of attachment to the shoulder girdle being the **glenoid region,** that on the pelvis the **acetabular region.**[1] These regions serve to separate dorsal and ventral parts in each girdle, a **scapular region** above the glenoid and a **coracoid** region below it in the pectoral girdle; while in the pelvic girdle these are an

[1] In fishes the articular surfaces of the girdles are convex or cylindrical; in Tetrapoda are usually excavate and cup-shaped and then are called **glenoid fossa** and **acetabulum** respectively.

upper **iliac** and a ventral **ischio-pubic** region. In the cartilage stage each girdle is perforated ventral to the articulation of the free limb for nerves going to the appendage, a **supracoracoid foramen** in either half of the pectoral girdle, an **obturator foramen** in the pubic (anterior) part of the ischio-pubic region.

Several bones may ossify in either half of the cartilage girdles. One extreme of this results in the formation of the following bones in either half: Pectoral girdle, dorsal to the glenoid region is a **scapula** (shoulder blade), extending upwards from the glenoid, its upper part often persisting as a separate bone, the **suprascapula.** In the coracoid region is an anterior **pre-** (or **pro-**) **coracoid** and a more posterior
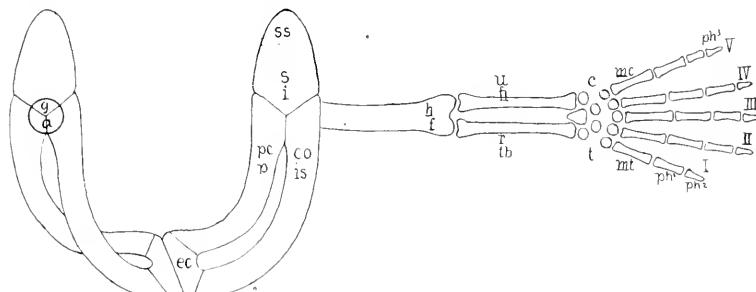
Fig. 242.—Diagram of Tetrapod girdles and appendages, posterior view. Upper letters, pectoral appendage; lower, pelvic appendage; *a*, acetabulum; *c*, carpus; *co*, coracoid; *ec*, epicoracoid (no equivalent in pelvis); *f*, femur; *fi*, fibula; *g*, glenoid fossa; *h*, humerus; *i*, ilium; *is*, ischium; *mc*, metacarpus; *mt*, metatarsus; *p*, pubis; *pc*, precoracoid; *ph*, phalanges, numbered; *r*, radius; *s*, scapula; *ss*, suprascapula (no equivalent in pelvis); *t*, tarsus; *tb*, tibia; *u*, ulna; I–V, digits.

coracoid bone (metacoracoid), these meeting in the glenoid region and having a considerable gap (**coracoid fenestra**) between them. The medial (ventral) ends of precoracoid and coracoid may be united by an **epicoracoid** cartilage or bone. With ossification the supracoracoid foramen is usually included in the coracoid bone.[1]

To this pectoral girdle of cartilage origin, bones arising in membrane may be added, thus forming a secondary girdle, reinforcing or even replacing parts of the cartilage girdle. These are best

[1] The nomenclature of the coracoidal elements is confused. The name coracoid was first given to a process of the human scapula which was soon recognized as arising from a centre apart from the scapula. Later an additional centre was found in the coracoid of mammals, all three centres persisting as separate bones in some species. Adult Monotremes have two distinct bones (fig. 273) in the same position as the rudimentary elements of higher mammals, and Cuvier applied the name coracoid to the posterior of these, calling the anterior the epicoracoid. Amphibia and many reptiles having two bones in the same relative position as the Monotreme coracoid and epicoracoid, the

developed in some fishes and tend towards reduction or absolute loss in some Tetrapoda.   In some Ganoids (sturgeon, etc., fig. 243) these bones are clearly dermal—parts of the skin—and as their homologues are evident in other forms, it is clear that they are phylogenetically derived from dermal ossifications, no matter how deep they may lie. Most prominent of these bones and persisting longest is the **clavicula**[1] which overlies more or less of the anterior ventral part of the coracoid cartilage and above this is the **cleithrum** which may extend dorsally over the scapular cartilage.   The clavicles of the two sides may meet in the middle line, or sternum or episternum (membrane) may inter-vene.   There may be a **postclei-thrum** posterior to the cleithrum, while the series of membrane bone may be continued dorsally by one or two **supracleithra,** the more dorsal of these (supracleithrum or posttemporal) being intimately connected with the posterior part of the skull, anchoring the girdle more firmly.   Outside of Tele-ostomes (and possibly some Thero-morphs—Cotylosaurs are said to have a cleithrum), none of these membrane bones, clavicle and episternum excepted, are known.

Fig. 243.—Posterior and lateral views of left half of shoulder girdle of *Acipenser sturio* (Butschli, '10).   Permanent carti-lage finely stippled; cartilage bones, coarse stippling; membrane bones white. *cl*, clavicle; *cm*, cleithrum; *corac*, cor-acoid; *g*, glenoid area; *N*, nerve through coracoid foramen; *pc*, postcleithra; *sc*, supracleithra; *ss*, suprascapula.

Usually three cartilage bones develop in either half of the pelvic girdle (fig. 242), an **ilium** dorsal to the acetabulum, ventral to

anterior of these being universally called precoracoid (or procoracoid), while the name epicoracoid is applied to a cartilage (or bone) uniting the medial ends of these two.

Adherence to the 'law of priority' would necessitate a change of names in the lower groups, but the priority fetich should not be allowed to cause greater confusion than now exists, when by setting it aside, greater simplicity may be had.   This would involve only a change of epicoracoid to precoracoid in the Monotreme.   The fact that the human coracoid process is a double structure does not necessitate the term metacoracoid for the posterior element of the lower orders.

[1] Earlier writers identified the more dorsal of the piscine bones overlying the girdle as the homologue of the human clavicle.   Restoring this name to the proper bone (**infraclavicle** of the earlier terminology) the bone formerly called clavicle is the clei-thrum, while in the same way the **supraclavicula** become the **supracleithra,** the post-temporal being the upper supracleithrum and the **postclavicula** the **postcleithrum.**

it an anterior **os pubis** (often containing the obturator foramen) and posterior to this an **ischium,** all three bones usually meeting in the acetabulum. The ventral bones often inclose a large ischio-pubic fenestra with which the obturator foramen may be united. Pubes and ischia of the two sides may meet by symphysis in the mid-ventral line, a symphysis of pubes being more common than one of ischia. More or less cartilage may persist in the symphysis, and in this a median **epipubis** may ossify in front, a **hypoischium** behind. Sometimes an **acetabular bone** occurs between ilium and pubis, this entering the acetabulum and occasionally excluding the pubis from articulation with the free appendage; usually acetabular bone and pubis fuse. There is no distinct ventral bone corresponding to the episternum and no membrane bones are known in the pelvis.

There is a close parallel between pectoral and pelvic girdles, especially in Tetrapoda. Each has three rami in either half, one dorsal and two ventral to the articulation of the limb, all preformed in cartilage, and each girdle with a nerve foramen in either half. The resemblance is strengthened if presternum be compared with either epipubis or hypoischium, accordingly as pubis or ischium be regarded as equivalent to coracoid.

Free Appendages

The skeletons of the free appendages of fishes and Tetrapoda differ more than do their girdles. The paddle-like paired fins (pterygia) of fishes do not support the body, but act more like rudders, while the podia support the weight and are also the chief locomotor organs. The pterygia of fishes have numerous rods (radialia and actinotrichia) to support a broad flexible membrane which does not bend sharply. Hence the radialia are usually jointed, with limited motion between the articles; the actinotrichia are flexible, and the intrinsic muscles of the fin are scanty. Podia, on the other hand, must be more slender, with fewer and firmer parts, the joints between them allowing great flexion and extension, and there must be more and stronger intrinsic muscles to cause motion of part on part and to hold parts firmly when necessary.

FISHES.—As the extent of differentiation of girdles and appendages of fishes is slight, and as pectoral and pelvic members differ but little, all are treated here together. Usually the pelvic fin is smaller than the pectoral, in correlation with its lesser use. Both girdles arise from paired cartilages and the individuality of the halves persists more often in the pelvis of Teleostomes than in Elasmobranchs,

while all but universally the pectoral halves are connected in the middle line.
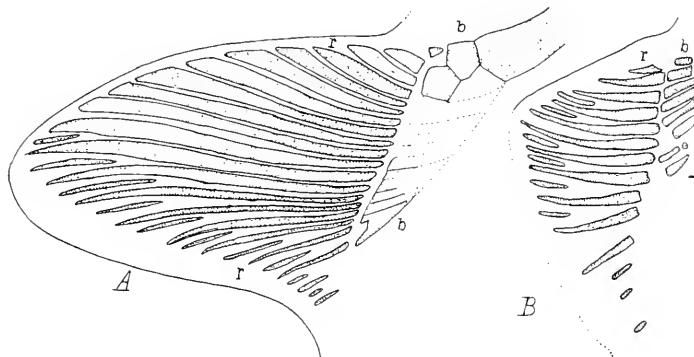
Fig. 244.—*A*, pectoral and *B*, pelvic fins of *Cladoselache* (Dean, '94). *b*, basalia; *r*, radialia.

The Devonian shark *Cladoselache* (fig. 244) presents a primitive condition. Its pelvic fin contains a series of radialia, strikingly like those of a median fin, some being in line with rod-like basalia, others connected with larger elements, apparently fused basalia. The anterior basals of the two sides approach each other in the midventral line and only need to meet to form the ischio-pubic bar of a true girdle. The fusion of the basalia of the pectoral girdle has gone farther, but the two halves have not met. *Chlamydoselachus* (fig. 245) has the basalia of the pelvic fin fused to a long puboischium, perforated by several nerves, the foramina possible indications of the compound character of the cartilage. With this pelvis a number of radialia are connected directly; those farther back are articulated to two elongate cartilages (fused basalia of this part of the fin), forming a **basipterygium**.
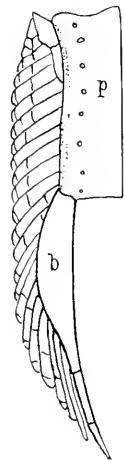
ELASMOBRANCHS.— The pectoral girdle of most Elasmobranchs is U-shaped (fig. 242). The glenoid surface (usually a ridge) separates scapular and coracoid regions which afford origin for the fin muscles. The supracoracoid foramen is near the ridge and in Raiæ (fig. 246) the nerve divides within it, emerging on the outer surface by two foramina. The scapular part extends far up

in the body wall and sometimes (*Acanthias, Xenacanthus*, etc.) bears a suprascapula. Its dorsal border is free in sharks; in skates is connected (by ligament or directly) with the anterior vertebræ. Several genera (*Acanthias, Heptanchus*) have a distinct cartilage (possibly presternal, p. 52 between the coracoid regions of the two sides.

A few sharks have the halves of the pelvic girdle separate through life; in only a few does it remain a broad plate; elsewhere it is a bar with the articular surface on the posterior side to accommodate the posteriorly directed fins. Skates (fig. 248, *A*) often have a prepubic process a little medial to the acetabular surface and extending downwards and inwards. There is usually a single obturator foramen, but in *Chlamydoselachus* (fig. 245) and Holocephala there are several, variously arranged.

FIG. 246.—Inside of half of pectoral girdle of *Myliobatis* (Gegenbaur, '65, modified). *c*, *s*, coracoid and scapular regions; *g*, posterior glenoid process; *n*, nerve.

In sharks whose development is known, after the union of the pelvic cartilages of the two sides, the pelvic girdle is at first U-shaped with well developed iliac region, which tends to disappear while the ischio-pubic part becomes a straight bar. The iliac portion remains large in skates (fig. 248, *A*) and Holocephals.

Since their functions are much alike, pectoral and pelvic fins of sharks are very similar. Both have jointed radials which either articulate with the girdle or with one, two or three basal cartilages, these articulating in turn with the girdles. The pectoral fin is the larger and there are some other differences. Some sharks (*e.g.*, *Scymnus*) have a single basal cartilage (**basipterygium**) on the postaxial side to which all of the radials are attached. Other sharks, with larger pectorals, have more numerous radials, some of which may articulate directly with the girdle. In such cases the basal part of at least one anterior radial is enlarged, forming a second basal element of the fin, the **propterygium** (fig. 247); in still others the propterygium is clearly the fused basals of several rays; in these the other basal is called the **metapterygium.** A farther specialization results in a **mesopterygium** between the pro- and metapterygia (fig. 247, *A*). The radials are usually divided transversely, the number of articles varying, and sometimes the distal ends are split, giving

more support to the margin of the fin, this being most common in
skates. A fusion of adjoining radials is common.   The radials of
sharks extend to about the middle of the fin, the distal parts of which
are supported by actinotrichia (ceratotrichia), more numerous than
the radials.   These are lacking in skates where the radials reach to
the border of the fin.
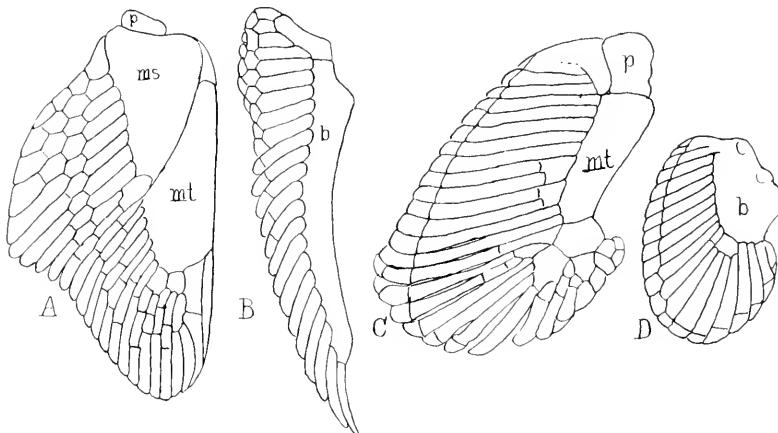
Fig. 247.—A, B, pectoral and pelvic fins of *Heptanchus cinereus;* C, D, pectoral and
pelvic fins of *Callorhynchus* (Mivart, '79).   b, basipterygium; *ms*, mesopterygium; *mt*,
metapterygium; *p*, propterygium.

The pectoral fins of skates (Raiæ) have several peculiarities.   They are
attached through life in the primitive horizontal position, correlated with the
mode of swimming.   More somites than usual enter the fin, which extends from
the pelvic fin to the head, although not all of the corresponding somites are
involved in it.   The fin skeleton is also extended forwards by several cartilages
at the tip of the propterygium, each bearing radials.   The most anterior of the
series is connected by ligament with a 'skull-fin cartilage' (a separate part of
the antorbital cartilage) which, in turn, is connected with the cranium, support-
ing the anterior part of the fin.   In some skates the middle radials of the fin
articulate directly with the girdle.

Most Elasmobranchs have two basal cartilages in the pelvic fin,
an anterior **propterygium** and a posterior **basipterygium** (**metaptery-
gium**) the latter always articulating with the pelvic girdle and
usually with the propterygium also when large.   In *Chlamydoselachus*
(fig. 245), *Xenacanthus*, etc., some of the anterior radials are attached
directly to the pelvis.   Many genera have the fasipterygium con-
tinued distally by a series of radial-like joints.   The pelvic fins of

Holocephals (fig. 247, *C*, *D*) are simple, having but a basipterygium which supports all of the few radials.

In the males of most Elasmobranchs (including the Holocephals) one or more radialia near the end of the basipterygium are modified to form the skeleton of the **mixipterygium** or 'clasper,' an organ used in copulation. The form and number of parts of the mixipterygia differ in different genera (fig. 248).

In both pairs of fins the radials usually occur only on the preaxial side of the basal cartilages, but in a few genera there are some radials
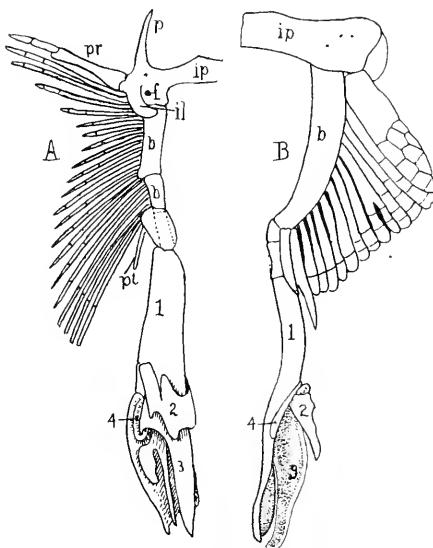
FIG. 248.—Skeletons of pelvic fins of (*A*) *Raia* (Goodrich, '09) and (*B*) *Heterodontus* (Daniel, '15) showing claspers (mixipterygia). *b*, basipterygia; *f*, obturator foramen; *il*, iliac process; *ip*, ischiopubic region; *p*, prepubic process; *pr*, *pt*, pre- and postaxial radials; 1–4, cartilages of clasper.

on the postaxial side (fig. 247, *C*, *D*), giving the distal part of the fin a distinct biserial arrangement, this playing a large part in the 'Archipterygial Theory' of the fin (p. 241).

The pelvic fins of Holocephals (fig. 247, *C*, *D*) are simple, having but a single basal (basipterygium) which supports all of the few radials. In the pectoral fin all three basals are present, but the propterygium alone (*Rhinochimæra*) or largely (*Chimæra*) is the element articulating with the girdle.

TELEOSTOMES.—The modifications of the appendicular skeleton in the higher fishes does not keep pace with the systematic posi-

tion as determined by other structures, but there is an advance over
Elasmobranchs, especially in the appearance of bone (both cartilage
and membrane) in the girdles, as well as in the modification and
reduction of the elements of the free appendages.

GANOIDS.— In girdles, as in other structures, the Chondrostei
are apparently primitive in the absence of cartilage bones and in the
independence of the two halves of the girdles.   The sturgeons (fig. 243)
show clearly the origin of the membrane bones, the only ossifications
of the girdles, which are more or less evidently repeated in all higher
fishes.   The cartilage girdle persists as such through life.   The
pectoral girdle has its halves connected by cartilage in the mid-
ventral line, the connexion being strengthened by the more external
membrane bones.   The supracoracoid foramen is divided as in
skates (p. 232) and there is a large fenestra in the coracoid region
which is repeated in many Teleosts.   The scapular region is strong,
and is continued dorsally by a suprascapular cartilage, connected
by ligament with the cranium.

The membrane bones of the pectoral girdle show from the surface
and are clearly a part of the integument.   The clavicle lies on
the ventral side of the coracoid region, those of the two sides meeting,

in some species, in the middle
line; in others they are con-
nected by a dermal **inter-
clavicle,** which recalls the
reptilian episternum.   This
ventral union strengthens a
girdle, weakened by the inde-
pendence of the coracoid
parts.   The cleithrum meets
the posterior side of the
clavicle and extends up on
the outer posterior side of
the scapular cartilage.   Be-
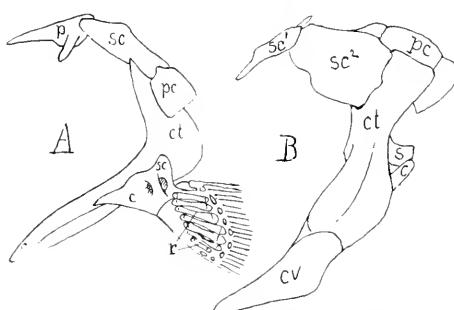
FIG. 249.—Pectoral girdles of (*A*) *Amia* (Good-
rich, '09) and (*B*) *Polypterus* (Gregory, '15). *c*,
coracoid; *cl*, cleithrum; *cv*, clavicle; *p*, post-
temporal (supracleithrum); *r*, radialia; *s*, scap-
ula; *sc*, supracleithra.

hind it are one or two small elongate postcleithra.   The dorsal
end of scapula and suprascapular cartilage are overlaid by a series
of two supracleithra, the upper of which (**posttemporal** of authors)
enters the posterior dorsal wall of the cranium.   In Cyprinoids and
Ganoids the supracleithra may also connect by ligament (sometimes
ossified) with the first vertebral centrum.

Polypterus (fig. 240, *B*) has an ossified scapula, the ossification involving the glenoid surface, ventral to which is a coracoidal ossification. Cleithrum and clavicle are fused, respectively, with scapula and coracoid, the cleithrum being the larger and extending over the narrower part of the clavicle. *Calamoichthys* has no cartilage bones.

The girdle is relatively smaller in Holostei than in other ganoids, both scapula and coracoid being reduced. *Lepidosteus* has a slight ossification around the glenoid surface; it is lacking in *Amia*. The cartilage has the same fenestra as have sturgeons. *Lepidosteus* has both clavicle and cleithrum; *Amia* has but a single bone, probably cleithrum, but possibly containing the clavicle (fig. 240, *A*).

TELEOSTS (fig. 250) show considerable differences in the pectoral girdles, and many genera need more study. The cartilage girdle is smaller than in Chondrostei. In Physostomes three bones ossify on either side: scapula, coracoid, and a third, dorsal to the coracoid and posterior to the scapula which has been called a **mesocoracoid,** this not appearing in most other teleosts. The plate-like scapula is largely dorsal to the glenoid region; it contains the supracoracoid foramen. The coracoid extends downwards and forwards and may aid in supporting the fin. When neither scapula or coracoid connect with the fin, the latter is articulated directly with the cartilage. Ventrally the coracoids of the two sides may meet, but sometimes an isolated cartilage intervenes.

The membrane bones are, in general, like those of the sturgeon. Physostomes have a single bone (cleithrum?) in the position of clavicle and cleithrum of other

FIG. 250.— Pectoral girdles of (*A*) *Trigla* (Gegenbaur, '64); (*B*) *Pleuronectes* (Cole and Johnstone, '01), and (*C*) *Gadus* (Bütschli, '10); *D*, base of fin of *Pimelodus* (Gegenbaur, '64). *c*, coracoid; *cl*, clavicle; *fr*, finrays; *l*, lepidotrichia; *pc*, post-cleithrum; *r*, radialia; *s*, scapula; *sc*, supracleithrum; *sp*, spine.

Teleosts. The clavicles in other groups usually extend medially and forwards and may meet. In some Teleosts, where the body is encased in a firm armor (South American Siluroids, Plectognaths and Lophobranchs), other bones may lie between the clavicles of the two sides

and may even extend over them. Clavicle and coracoid are often intimately united. The main part of the cleithrum is dorsal to the glenoid surface, but it may extend down over the upper part of the clavicle.

The girdle is usually connected with the cranium by one or two suprascleithra, the distal one usually being forked (fig. 250, C) one ramus articulating with the epiotic, the other with opisthotic or exoccipital, and rarely (Cyprinoids) with the first vertebral centrum. In some cases the dorsal supracleithrum is intercalated in the dorsal surface of the cranium, lateral to the dermoccipital and forms the true posttemporal. A few Siluroids lack supracleithra, the cleithrum articulating with the cranium, while in eels, which also lack supra-
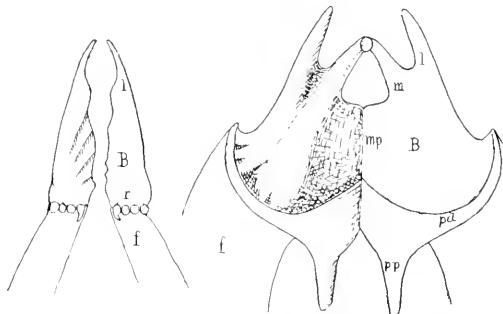
FIG. 251.—Pelvic girdles of (A) *Clupea* and (B) *Amiurus* (Kolzow, '96). *B*, basal; *f*, fin; *m*, median crest; *mp*, median process; *pd*, dorsal process; *pp*, posterior process.

cleithra, girdle and skull are connected only by ligament. Most Teleosts have from one to three postcleithra; when several occur they extend in an oblique line downwards from a point behind the connexion of cleithrum and supracleithrum. In the 'Thoracici' (p. 228) the lower end of this series may reach the basal ossicle of the pelvic fin.

In the lower Ganoids and Teleosts a pair of triangular elements extend inwards and forwards from each pelvic fin (fig. 251). These are cartilage in *Sturio*, elsewhere ossified to varying extents. In most Ganoids (Holostei excepted) they do not meet in the median line, but they are connected in some sturgeons and in *Polypterus* by a median cartilage which may represent the true pelvis. In Teleosts the range of form is greater. The basal parts may be connected by ligament or may be in contact. Many have a second process on the medial side, arising at about the level of the articulation of the

fin, which forms a second symphysis by meeting its fellow. Occasionally the anterior symphysis is lost, or the two symphyses may lengthen so that the two halves meet in their whole length.

In most Ganoids and Teleosts these structures do not form a true pelvis, the basal parts of the fin being, as Chondrostei show, basipterygia, formed of the basal parts of several radialia, and the median cartilage of *Polypterus* and some Sturionids may be the only true pelvic structure. Only on such a basis can the development of the girdle in Elasmobranchs and higher fishes be compared. The position of the pelvic fins in 'Thoracici' and 'Jugulares' was referred to above (p. 228), the pectoral and pelvic girdles being connected by ligaments or occasionally (*Astroscopus*) may be firmly united.

The paired fins of Teleostomes differ from those of Elasmobranchs in several points. The number of radialia and their size is reduced, and, except in a few Ganoids and Dipnoi, there is little in the pectoral fin to compare with the three basal plates of sharks, most of the radials articulating directly with the girdle. The fins themselves are largely supported by flexible, little ossified lepidotrichia like those of the median fins; they are usually divided transversely into small blocks. Ceratotrichia may also be present.

The pectoral fins of Ganoids have both pro- and metapterygia; those of Crossopterygians (fig. 252) have a large mesopterygial cartilage, slightly ossified in the centre, between them. In other genera the place of this is taken by several radials which articulate directly with the girdle. *Acipenser* has a large dermal bone on the preaxial side of the fin, with which the propterygium is closely connected; this is followed by several radials, more

FIG. 252.—Pectoral fin of *Polypterus* (Gegenbaur, '64); bone white, cartilage stippled. *ms*, mesopterygium; *mt*, metapterygium; *p*, propterygium; *r*, radialia.

numerous distally, as in many Elasmobranchs. Sometimes the anterior margin of the fin has an ossified spine.

The ventral fin of most Ganoids has a large basal element (called a basipterygium, in *Acipenser* more like a propterygium) apparently formed by the fusion of several basalia, and bearing a few radials, sometimes ossified only in the middle. *Calamoichthys* lacks ventral fins.

The fin skeletons of some fossil Ganoids (fig. 258) is interesting as suggesting the way in which the podia of Tetrapoda have been evolved (p. 245).

Teleosts (fig. 250) have few radials (rarely more than five, sometimes but two or three) in the pectoral fin. These may be elongate (Physostomes) or small plate-like particles, articulating or even uniting with the pectoral girdle between scapular and coracoid parts, the hinge of the fin lying between them and the actinotrichia. Often there are small cartilages between radials and actinotrichia. Many Acanthopterygii have an ossified spine at the anterior margin of the fin. The ventral fins of Teleosts usually lack radials; when present (some Physoclists) they are small.

DIPNOI have the pectoral girdle less specialized than in Teleosts. The development is imperfectly known, so there is uncertainty as to the elements. The cartilage stage is much like that of normal Teleosts, the cartilage halves uniting in the median line. There is a single ossification in the glenoid region of *Protopterus* and *Lepidosiren*, two in *Ceratodus*, scapular and coracoid in position, but usually called cleithrum and clavicle, although it is not known whether they be cartilage or membrane in origin. As in Teleosts the girdle is connected with the cranium by one (*Ceratodus*) or two supracleithra (*Protopterus*, *Lepidosiren*).

There is a true pelvic girdle, continuous from side to side, with a prepubic process on either half and a slender epipubic bar extends forwards from the ischio-pubis. The pelvis arises from paired cartilages.

FIG. 253.—Pelvic fin and part of girdle of *Ceratodus* (David-off).

The three existing Dipnoan genera differ considerably in fin structure. *Ceratodus*, the more primitive, has pectorals and ventrals nearly equal, and the skeletons of the two are more alike than is usual in fishes. Each has a jointed axis, the joints becoming smaller distally. The basal joints lack radials, but all others have them on either side, the fin being biserial (fig. 253). The radials support actinotrichia which extend nearly to the margin of the fin. The pectoral radials are more numerous on

the preaxial, those of the pelvic fin on the postaxial side, the pre-
axials being reduced in size and number. *Lepidosiren* and *Protopterus*
have retained only the jointed axis, all radials being lost.   The paired
fins of fossils which are clearly Dipnoan show no essential difference
from *Ceratodus*.

The fins of *Ceratodus* represent Gegenbaur's archipterygium, and play a
most important part in his theory of appendages, of which biseriality is the very
essence.   It is more probable that biseriality is not primitive, but is the extreme
of conditions in some sharks.   It is a question whether the axis of the Dipnoan
appendage is a radial or the homologue of the metapterygium of Elasmobranchs.

THE ORIGIN OF VERTEBRATE APPENDAGES

Two prominent hypotheses attempt to explain the origin of the paired
appendages of Vertebrates, the fin-fold theory of Thacher, supported later by
Mivart and Balfour, and the gill-arch or archipterygial theory of Gegenbaur.
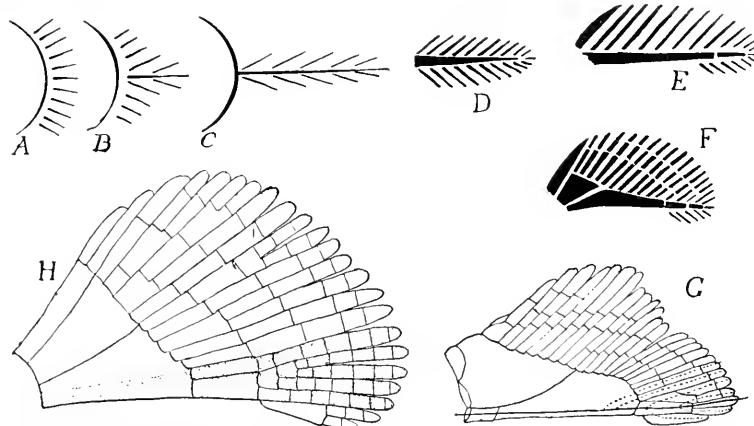
Fig. 254.—Diagrams illustrating theories of origin of paired limbs. *A–G*, archi-
pterygial theory; *H*, another view.   *A*, typical gill arch and gill rays; *B*, outgrowth of
middle radial, drawing with it adjacent rays; *C*, gill arch a girdle, rays now forming a
biserial appendage as in *D*; *E*, loss of most postaxial radials; *F*, formation of basal
cartilages of pectoral fin; *G*, origin of Tetrapod appendage from fin, persisting parts with
dotted lines; *H*, persisting parts stippled.

Both agree that the fins of fishes are more primitive and ancestral to the legs of
Tetrapoda.   The first theory regards both median and paired fins, which have
many points in common, as having a common ancestry.   The archipterygial
theory, at least by implication, denies any homology between the two and only
tries to account for the paired appendages.

The archipterygial theory is based on the biserial fin of *Ceratodus*, its girdle
bearing the axis which bears radials on either side.   This is the **archipterygium**
and from it he believes that all paired appendages of Vertebrates—pterygia and
podia—have been derived.   He argues that the archipterygium and its girdle
have developed from a gill septum like that of an Elasmobranch (fig. 254, *A*),

its skeleton coming from the branchial arch and its rays. Each septum is supported near its inner wall by an arch from which rays extend into the lateral part of the septum. Lateral growth of the septum would produce a fin-like process and would draw the radials out into it, the medial ray forming an axis, those above and below becoming arranged on either side of it (fig. 254, *C*, *D*). Jointing of the axis would give a skeleton like that of the fin of *Ceratodus*. Migration caudally of two such modified septa along the sides of the body would furnish pectoral and pelvic fins.

Somewhat allied to this (and subject to the same objections) is the view that the paired appendages have come from external gills like those of Amphibia.

To the part of the archipterygial theory outlined above, several objections have been advanced and have been practically ignored by its author in his last presentation of the subject. Briefly these are:

(1) Development shows (fig. 70) that the branchial arches arise in the splanchnic wall of the cœlom of the branchial region; while the girdles of the appendages are clearly somatic in origin, arising lateral to the cœlom. Hence the two cannot be equivalent.

(2) The gill septum, as shown by myotomes, blood vessels, nerves and skeletal parts does not include structures from more than a single metamere, while paired appendages—both pterygia and podia—are by the same test, polymeric, arising from several somites (fig. 240).

(3) The archipterygial theory demands that the primitive line of attachment of appendage to trunk shall be vertical; according to ontogeny, whatever the adult condition, the original attachment is horizontal, extending over several somites.

(4) There is not the slightest evidence of such shifting over several or many somites as the theory demands, especially for the pelvic member, and the innervation totally negatives any such hypothesis. The appendages actually arise from the same somites with which they are connected in the adult, and the nerves are those of the corresponding segments.

(5) Ontogeny and paleontology agree that the biserial condition is secondary and not primitive.

(6) The gill-arch theory does not explain the several resemblances between median and paired fins.

The alternative (fin-fold) theory assumes that the ancestral vertebrate had two longitudinal folds, one more dorsal, the other more ventral, on either side of trunk and tail. These folds were supported by metameric skeletal rods like the radials of primitive fins. The folds migrated, the upper towards the dorsal surface, the ventral in the opposite direction (fig. 255). There being no obstruction to the dorsal migration, right and left folds met in the mid-dorsal line, forming a continuous fin along the back from head to tip of tail. Behind the anus, in the same way, the ventral folds would form a similar median fin on the ventral side of the tail.

The anus, however would prevent the ventral folds meeting at that point, and the influence of that opening prevented their meeting farther forwards, so that there resulted paired folds on the lower lateral sides of the trunk, while the

use of these folds in controlling the direction of motion was an additional agent in preventing their union. From the median folds arise, dorsal, caudal and anal fins, while from the paired folds on the lower side of the trunk, pectoral and pelvic
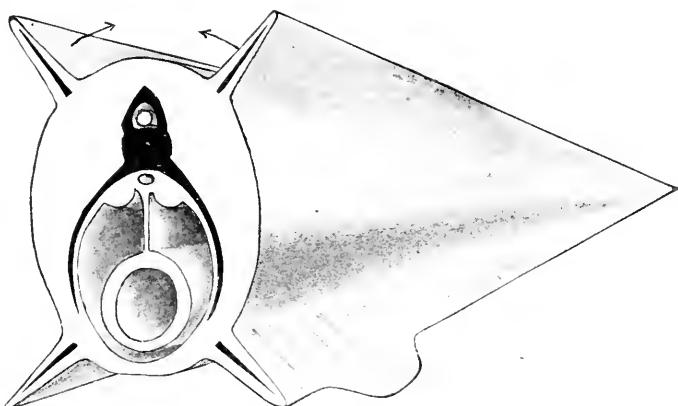
FIG. 255.—Diagram of origin of median and paired appendages from lateral fin-folds.

fins have arisen, by the hypertrophy of parts and the obsolescence of the inter-vening tracts. To this theory the objections are:

(1) Ontogeny and paleontology show no evidence of the origin of median fins from paired folds, except that the muscles are paired in origin, arising from
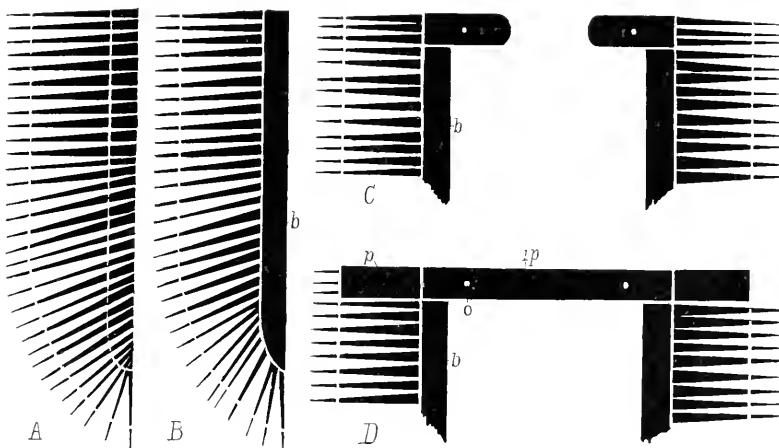
FIG. 256.—Thacher's figures illustrating his theory of the origin of the pelvic girdle by fusion of the basal elements of primitive paired fins. *b*, basipterygium; *ip*, ischio-pubic bar; *p*, propterygium; *o*, obturator foramen.

buds from the upper borders of the myotomes, just as do the muscles of the paired fins from their lower borders (fig. 240). Then the actinotrichia and the dermal bones of the median fins also are paired in origin.

(2) The most primitive Chordates (*Amphioxus* and the Cyclostomes) show no trace of paired appendages, save the improbable suggestion that the meta-pleural folds of the former, and folds near the anus of *Petromyzon* be such.

(3) The deeper parts of the skeleton of the median fins (basalia and radialia) are unpaired in development.

(4) Except the embryo of *Torpedo*, no Vertebrate is known to have such longitudinal folds in the trunk region as the hypothesis would imply.

On the other hand a variety of the Japanese goldfish has fins which are in full harmony with the view that the median fins are double in origin, both anal and caudal sometimes being double throughout, a condition explicable on the assumption that these normally azygous appendages have had a paired ancestry. The skeleton of the more primitive paired fins (*e.g., Cladoselache*, fig. 244) is
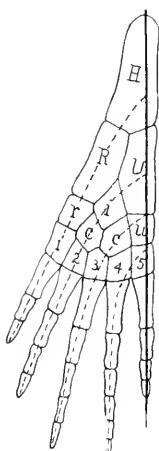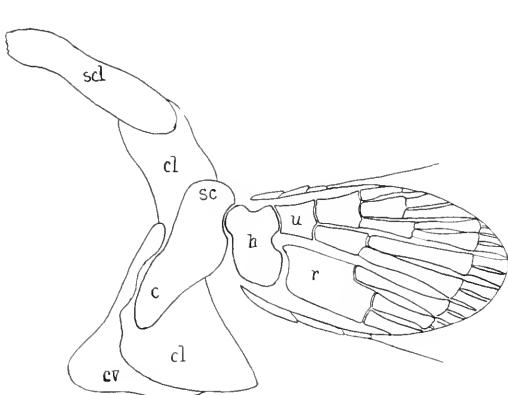
FIG. 257.   FIG. 258.

FIG. 257.—Fore foot of Amphibian showing relations of persisting parts with archi-pterygium (Gegenbaur, '77; compare with fig. 254). The heavy line is archipterygial axis, the dotted lines the uniserial radii on the preaxial side; the postaxial being lost. Later, Gegenbaur had other interpretations of parts.

FIG. 258.—Pectoral girdle and base of appendage of *Sauripterus* (Adams, in Gregory, '15). *c*, coracoid; *cl*, cleithrum; *cv*, clavicle; *h*, humerus; *r*, radius; *s*, scapula; *scl*, supracleithrum; *u*, ulna.

composed of metameric radials, some articulated to basal cartilages, others to plates, evidently the result of fusion of basals. Fusion of these plates of the two sides in the middle line would result in a pubo-ischiadic bar, while the necessity of a firm origin for the levator muscles of the fin would explain the iliac process of the pelvis. The same conditions in front would give the shoulder girdle and the skeleton of the pectoral fin.

The second problem of the paired appendages concerns the evolution of the Tetrapod podia from the pterygia of fishes. That podia and pterygia are broadly homologous is self evident, but the steps by which the latter have been trans-formed into the jointed limbs of the higher Vertebrates are still very uncertain.

Gegenbaur recognises the archipterygial axis in that of the Tetrapod append-age (fig. 257). The Elasmobranch fin has largely lost its biserial character (best shown in *Ceratodus*) only a few of the postaxial radials persisting while many preaxial radials remain (fig. 254, *F, G*). In the transformation of the fin into a podium, a further loss of pre- and postaxial radials and of all basalia except the metapterygium, which forms the stylopodial part of the limb. Two of the proximal radials furnish the zeugopodial elements; three of the next radials form the proximal basipodials and the more distal radials furnish the remaining parts of the typical pentadactyle foot, the relations of these being shown by dotted lines in figure 257. A variation of this has the axis passing through the second digit, regarding pollex or hallux as a postaxial ray.

Another view is that the podial bones have come from the fins of some Crossopterygian Ganoid (fig. 258) where the stylopodial and zeugopodial parts are readily recognized and where a reduction of the distal radials provides for the basipodial parts. Then the line between the Crossopterygian and the Elasmobranch pterygia is not unsurmountable.

APPENDAGES OF TETRAPODA

Pectoral Girdle

In the lower Tetrapoda the pectoral girdle, as preformed in cartilage, has scapular and coracoid parts, separated by the glenoid fossa with which the limb is articulated. With the change in the functions of the limb, the girdle differs from that of fishes in details. The two halves either meet in the middle line or are separated by the sternal structures with which they are connected. The girdle is rarely connected with the axial skeleton directly[1] the only connexion being indirect by way of the sternum and ribs. Except for this, the girdle is bound to other skeletal parts only by muscles and ligaments.

At most there may be the following bones in the pectoral girdle[2] —scapula, suprascapula, coracoid, precoracoid and epicoracoid of cartilage origin, while the only membrane bones are the clavicle (cleithra are lost above fishes, unless they persist in some Stegocephals and Cotylosaurs) and the episternum.

[1] Some Plesiosaurs are said to have the scapula connected with the anterior vertebræ; *Pteranodon* has it articulated with the neural spines of the fused anterior vertebræ. If the precoracoid of the Stegocephala be, as has been suggested, a supracleithrum, there may have been a connexion in this order. Crocodiles sometimes have the scapula attached by ligament to the first thoracic vertebra.

[2] Basing the argument on the fact that there are two coracoidal ossifications in mammals, the attempt has been made to show other homologies between the mammalian and reptilian girdles than those usually recognized and which are adopted here (see p. 229).

While it is possible to recognize broad homologies between piscine and Tetrapod pectoral girdles, there are difficulties in details and several of the statements below are only tentative. There is a striking degeneration and loss of parts in the higher groups—replacement of precoracoid by clavicle, disappearance of epicoracoid and episternum, reduction of coracoid, and in many mammals loss of clavicle.

AMPHIBIA.—Girdles are absent from Aistopod Stegocephals and Gymnophiona, while the diversity in other orders is greater than

in some other classes. The probably neotenic character of the Urodeles results in an almost embryonic condition of the girdle, membrane bones being absent, although probably present in the ancestors.

FIG. 259.—Pectoral girdle of *Eryops* (Gregory, '15). *c*, coracoid; *ct*, cleithrum; *cv*, clavicle; *e*, episternum; *sc*, scapula.

STEGOCEPHALA (Aistopoda excepted) have bones in the thoracic region. In some (fig. 259) there is a continuous coraco-scapula without indications of division; in front of this is a curved bone (clavicle or cleithrum), the broader medial end of which is ventral to the broad episternum. In other genera the identification of the separate bones (some apparently centers of ossification in larger cartilages) is not certain. The episternum
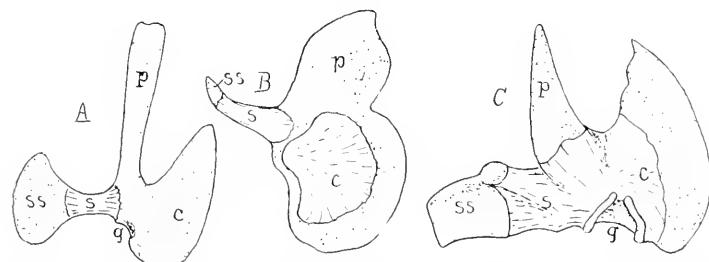
FIG. 260.—Pectoral girdles of (*A*) *Necturus*, (*B*) *Spelerpes*, and *C*, *Salamandrina* (Wiedersheim, '75). *c*, coracoid; *g*, glenoid fossa; *p*, precoracoid; *s*, scapula; *ss*, suprascapula. Cartilage stippled, bone lined.

(usually a rhomboid plate) is in the median line, with the broader ends of a pair of clavicles (? cleithra) ventral to it. Behind these is a pair of slender splints, interpreted as scapulæ, followed by a pair of larger, often semicircular, bones, possibly coracoids.

URODELES (fig. 260) have the cartilage girdle largely persistent, the ossifications in it being small; no membrane bones are present. The scapula is narrow, the precoracoid slender and directed forwards, while the larger coracoid is transverse, there being a large gap (**coracoidal fenestra**) between coracoid and precoracoid, the median ends of these elements being connected only by ligament, there being no epicoracoid except in *Siren* and *Cryptobranchus*. The median ends of the coracoids overlap as in the Arciferous Anura. The sternum is posterior to the girdle, its anterior border usually grooved to receive the posterior margin of the coracoids. There is usually a cartilage bone in the glenoid region, extending into the scapular part, but its ventral end, which contains the supracoracoid foramen, is clearly coracoidal. *Siren* has distinct scapula and coracoid, the upper unossified part of the scapula being usually called a suprascapula.

ANURA have a more typical girdle, scapula, precoracoid and coracoid being present, as is, except in *Dactylethra*, an epicoracoid (an unossified epicoracoid occurs in the related *Pipa*). The precora-
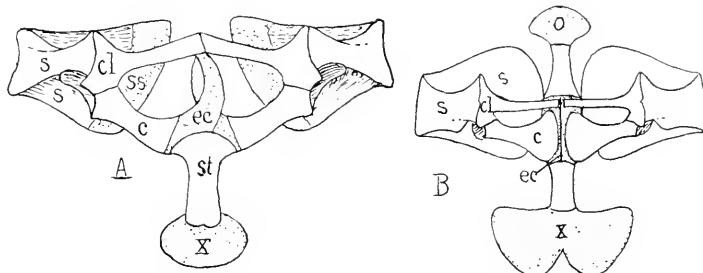
FIG. 261.—Pectoral girdles and sterna of (*A*) *Bufo americanus* and (*B*) *Rana catesbyana*. *c*, coracoid; *cl*, clavicle; *ec*, epicoracoid; *o*, omosternum; *s*, scapula; *ss*, suprascapula; *st*, sternum; *x*, xiphisternum.

coids differ from those of Urodeles in being nearly transverse; the coracoids are more slender and are directed a little backwards. In Arcifera (fig. 261, *A*) the epicoracoids of the two sides overlap, touching the sternum with their posterior borders. In Firmisterna (fig. 261, *B*) they abut against the sides of the sternum with which they are intimately associated. Precoracoid, epicoracoid and coracoid enclose a large coracoid fenestra on either side.

Ossifications of cartilage are more numerous than in Urodeles. Most of the scapular cartilage forms an osseous scapula, its upper part

largely calcifying or ossifying as a suprascapula (fig. 262). The distinct coracoid enters the glenoid fossa, the epicoracoid usually remains cartilage. The precoracoid (fig. 263) is peculiar in being largely or wholly replaced by the clavicle which grows over it from in front, so that it may persist as cartilage within the clavicle, may coossify with that bone, or may entirely disappear, except that parts
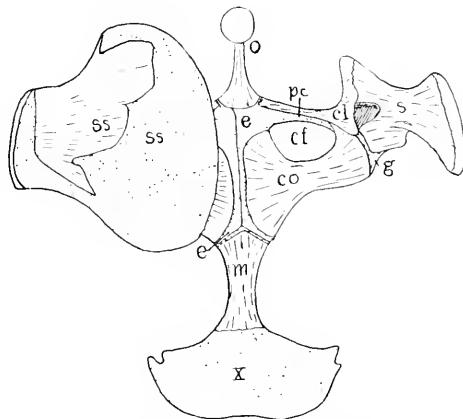
FIG. 262.—Pectoral girdle of *Rana temporaria* (Parker, '63). *cf*, coracoid fenestra; *cl*, clavicle; *co*, coracoid; *e*, epicoracoid; *g*, glenoid fossa; *m*, mesosternum; *pc*, precoracoid; *s*, scapula; *ss*, suprascapula; *x*, xiphisternum.

may persist as cartilage at either end of the clavicle in many frogs. The clavicles, the only membrane bones in the girdle, meet in the middle line, but do not enter the glenoid fossa. No true episternum is present, but in most Anura a pair of cartilages in front of the girdle ossify as a single bone of uncertain homology. This has been called
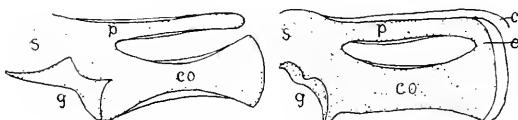
FIG. 263.—Two stages in development of pectoral girdle of *Rana esculenta* (Goette, '77). *c*, clavicle; *co*, coracoid; *e*, episternum; *g*, glenoid fossa; *p*, precoracoid; *s*, base of scapula.

omosternum and **presternum,** earlier episternum; it certainly is not the latter.

REPTILIA with a few exceptions (snakes and some footless lizards) have a pectoral girdle. Unfortunately little is known of the girdle of the ancestral group, the Theromorphs, and nothing concern-

ing the development of their bones. What is known is summarized below. Even among living reptiles there is difficulty in deciding which has the more primitive girdle.

RHYNCHOCEPHALIA.—*Sphenodon*, whose development is known, has each half of the early pectoral girdle as a continuous cartilage, perforated for the supracoracoid nerve (fig. 264). The cartilage extends to the clavicle and transverse arm of the episternum, and lacks gaps or fenestræ. The medial margins of the two sides meet in front, dorsal to the episternum, while the diverging posterior borders enclose the anterior sides of the sternum.

Ossifications in this cartilage form scapula and coracoid which fuse at the glenoid fossa. Aside from these there are no cartilage bones and not all of the cartilage is utilized in these, the rest of it
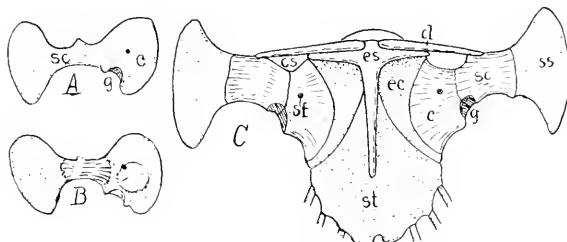
FIG. 264.—*A* and *B*, development of pectoral girdle of *Sphenodon* before and at the appearance of bone (Howes and Swinnerton, '01); *C*, adult (Furbringer, '00). *c*, coracoid; *cl*, clavicle; *cs*, coraco-scapular fenestra; *ec*, epicoracoid; *es*, episternum; *g*, glenoid fossa; *sc*, scapula; *sf*, supracoracoid fenestra; *ss*, suprascapula; *st*, sternum.

calcifyinp. The scapula is elongate rectangular, the clavicles are slender curved rods connecting scapula and episternum, the latter being T-shaped, the cross bar of the T being short and joining the posterior sides of the claviculæ.

Comparisons with Anura and Lacertilia make it probable that the part lettered *ec*, in figure 264 must be the epicoracoid, while that next the clavicle and lateral arm of the episternum is the precoracoid part. These relations can be carried to fossils like *Palæohatteria* and *Palæosaurus*, and from these it would appear that the interpretation of the Stegocephalan girdle (p. 246) is correct, allowances being made for the non-fossilization of the cartilage. The Thalattosauria had an oval plate-like coracoid and a narrow scapula.

SQUAMATA.—A pectoral girdle occurs only in Lacertilia and Pythonomorphs, snakes having lost it completely, while apodal lizards have it greatly reduced, or in a few genera entirely absent, all stages of reduction occurring in existing forms. In typical lizards

(fig. 265) the cartilage girdle is perforated by two or three fenestræ in the coracoidal part, one nearly in front of the glenoid fossa, and one or two medial to these; sometimes the scapular part has a fenestra. Two ossifications occur in this cartilage, one scapular, the other in the posterior part of the coracoid region. The scapula is continued dorsally by a cartilage (or sometimes ossified) suprascapula. The scapula frequently has a small acromial process. The large coracoid contains the supracoracoid foramen, and its
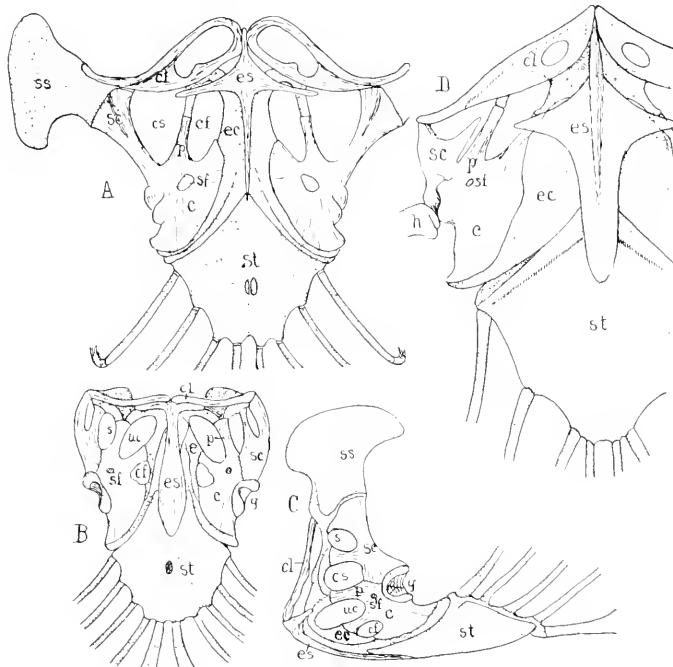
Fig. 265.—Pectoral girdles of (*A*) *Xantusia vigilis* (Camp, '23); (*B*, *C*) *Iguana tuberculata* (Parker, '68); and (*D*) *Sphærodactylus macrolepis* (Noble, '21). *c*, coracoid; *cf*, coracoid fenestra; *cl*, clavicle; *cs*, *s*, coraco-scapular fenestra; *e*, *ec*, epicoracoid; *es*, episternum; *g*, glenoid fossa; *h*, humerus; *p*, precoracoid; *sc*, scapula; *sf*, supracoracoid foramen; *ss*, suprascapula; *st*, sternum; *uc*, upper coracoid fenestra.

ossification usually extends to the bars between the fenestræ and into the glenoid region where scapula and coracoid fuse. The arcuate cartilage (epicoracoid region) nearest the median line remains unossified, these parts of the two sides meeting dorsal to the episternum. The anterior part of the cartilage (sometimes replaced by ligament), which limits the fenestræ in front is probably precoracoid, and this element may also include the lateral bar of the

coracoid fenestra. This interpretation, however, meets some difficulties.

The clavicle extends transversely, in front of the fenestræ, from scapula towards the median line, and may meet its fellow. Its medial end is often broad, these enlargements sometimes being fenestrated (fig. 265, *A*, *D*) and resting against the sternum, the anterior end of which bears a transverse bar on either side which may articulate with the clavicle, or when the episternum is T-shaped or cruciform, with the arm of the latter. Clavicle and sternum are frequently fused for some distance. When an anterior process is present the clavicle loses its connexion with the precoracoid and acts as a brace between scapula and sternum. The clavicle is purely a membrane bone and shows no such mixture as occurs in Anura. Its extension along the anterior side of the scapula recalls conditions in some fishes. The episternum is very variable in shape—rhomboid, T-shaped, cruciform, or rod-like. It always lies beneath the middle line of the sternum.

In less typical lizards there is a tendency towards reduction and simplification of the girdle. *Heloderma* and *Chamæleo* have a compact coracoid plate which meets its fellow (*Chamæleo* has lost episternum and clavicle), while the postero-medialb order enfolds the anterior sternal margin. There is a single fenestra anterior to the glenoid fossa and scapula and coracoid are continuous. In *Anguis* and some other apodal lizards the fenestræ become incisures by loss of the anterior border of the coracoid region, but even in Amphisbænids and *Aniella* (fig. 266) rudiments of coracoid and clavicle occur, although it is difficult to say whether the former be more coracoid than scapula. *Lepidosternon* and *Cephalotis* are said to have lost the girdle completely.

FIG. 266.—Girdle, sternum and ribs of a limbless lizard, *Aniella* (Camp, '23). *cl*, clavicle; *cs*, coraco-scapula; *s*, sternum (presternum).

The extinct Pythonomorphs usually lack the clavicle and episternum; when present they are rudimentary. The large flat coracoid has a fenestra or incisure, as well as a supracoracoid foramen. The coracoids are widely separated, possibly a broad epicoracoid cartilage was present. The scapula is broad triangular.

CROCODILIA.—The clavicle and precoracoid are lacking in modern crocodiles but present in Pseudosudia. *Crocodilus porosus* has a procartilage stage of a probable precoracoid. The coracoid is small and expanded at either end; no incisures occur, but there is a supracoracoid foramen. The slender rod-shaped episternum joins the

sternum (fig. 62). The scapula, expanded dorsally, is largely ossified and the suprascapula is small.

Belodon (extinct) has a short rounded coracoid and a single large fenestra; the scapula is moderate. The Mesosuchia have lost the clavicles, while the elongate coracoid contains a supracoracoid foramen.

CHELONIA differ from all other Vertebrates in the shifting of the pectoral girdle back under the dermal armor, a part of which is formed by the ribs. The girdle (fig. 267) consists of three rods, one dorsal and two ventral, all preformed in cartilage and meeting at the glenoid fossa. The interpretations of these differ. The dorsal rod is clearly the scapula; it has a small suprascapular cartilage and is connected by ligament or carti-lage with the anterior costal plate of the carapace. The anterior ventral bar forms a continuum with the scapula, and when an entoplastron is present, the ventral end of the rod is connected with it by cartilage or ligament. The second bar extends medially and backwards from the fossa; its medial end is expanded, but those of the two sides do not usually meet, although they overlap in *Dermochelys*. The medial ends of the ventral bars of a side are con-nected by ligament which is sometimes condrified.

FIG. 267.—Pectoral girdle and part of plastron of *Chelone midas* (Parker, '68). *c*, coracoid; *en*, entoplastron; usually re-garded as homologue of episternum; *ep*, epiplastron (less certainly homologue of clavicle); *hp*, hyoplastron; *pc*, precora-coid; *sc*, scapula.

The usual view is that the anterior ventral bar is the precoracoid, the posterior the coracoid, a view which receives confirmation, if the cartilage at times connecting these be the epicoracoid. Those holding this view recognize the episternum in the entoplastron, and often the clavicles in the epiplastra. (On this last point see below.) Another interpretation is that the anterior rod is a greatly developed acromion, no precoracoid being present. Others consider it, as in Anura, composed of both precoracoid and clavicle, although it contains no membrane bone.

The assumption of homology of clavicle and epiplastron involves phylo-genetic difficulties. Clavicles appear as low as the Ganoids, and it is easier to assume their loss in Chelonia than to suppose they have remained in the skin

as high in the scale as the turtles. The homology of episternum and entoplastron is more probable, since episterna appear in reptiles, none being known in Amphibia or lower, unless the Anuran omosternum be such, as has been suggested, a view which has its difficulty in that the omosternum has a cartilage origin.

THEROMORPHA (fig. 268).—Unfortunately nothing is known of the cartilage girdle, aside from suggestions of its former presence on the edges of certain bones. It is also unfortunate that our knowledge is so deficient with regard to so many of the adults. In general it may be said that clavicle and episternum are well developed, the former of the two sides often meeting in the middle line.
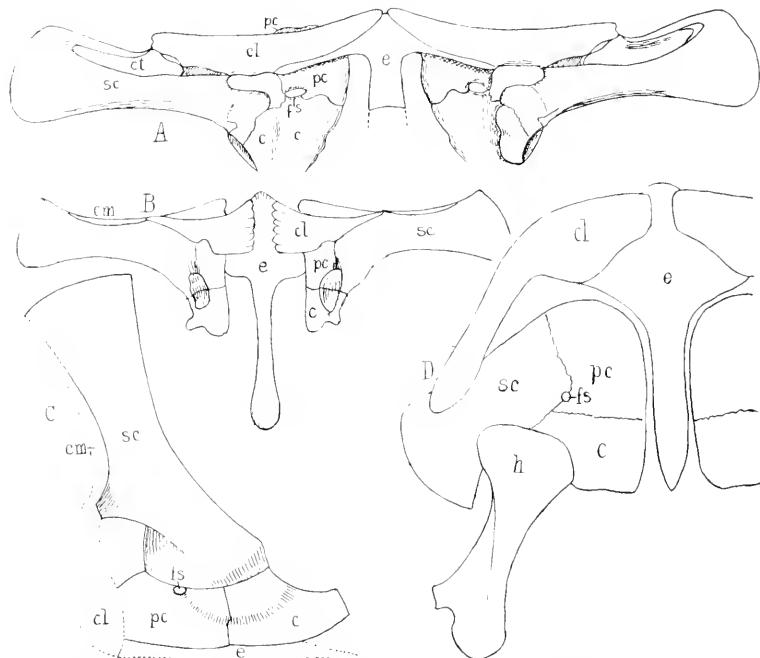
FIG. 268.—Pectoral girdles of Theromorphs. *A, Parieasaurus* (Seeley, '93–4); *B, Dimetrodon* (Case); *C, Udenodon* (Broom, '02); *D, Labidosaurus* (Williston, '08). *c*, coracoid; *cl*, clavicle; *cm*, *ct*, cleithrum; *e*, episternum; *fs*, supracoracoid foramen; *h*, humerus; *pc*, precoracoid; *sc*, scapula.

All parts are united by suture or by fusion and no motion seems possible between them. Scapula, coracoid and precoracoid surround no fenestræ, and in some there is evidence of an epicoracoid on the margins of the latter bones. The coracoids meet the anterior border of the sternum and the supracoracoid foramen perforates the precoracoid; the scapula was very long in *Pareiasaurus*. Coty-losaurs had a separate ossification in the position of the cleithrum of fishes.

ICHTHYOPTERYGIA have a strong lizard-like girdle. The scapula lacks a marked suprascapula, it and the coracoid forming the glenoid fossa. The large coracoids meet in a long symphysis in the middle line; each has a distinct emar-gination in its anterior border, and indications of a former cartilage (like a

precoracoid) in front, such as occurs in lizards, while the lateral end of the coracoid has two facets for articulation with scapula and humerus. The T-shaped episternum is small.

SAUROPTERYGIA (fig. 269), like many other aquatic vertebrates, have the scapula reduced to a small plate with a strong oblique dorsal process. In the latest Plesiosaurs the bone has disappeared except in the glenoid region,
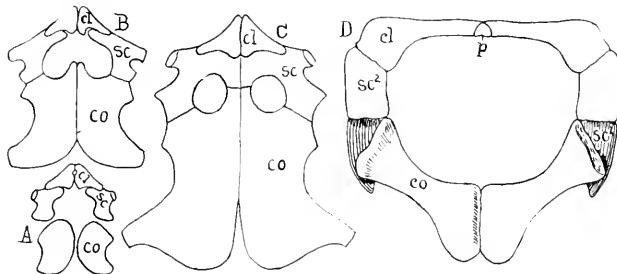
FIG. 269.—*A* to *C*, development of pectoral girdle of *Cryptocleidus* (Andrews, in Woodward); *D*, girdle of *Lariosaurus* (Deeke, '86). *co*, coracoid; *cl*, clavicle; *p*, presternum or episternum; *sc*, scapula. In *A* to *C*, note relative decrease in size of clavicle and meeting of coracoids of the two sides

from which a descending process connects with the somewhat rudimentary secondary girdle, a process which some compare with the anterior bar of Chelonians, the nearest relatives of the Sauropterygia. In more recent genera the coracoid, which has a rather broad median margin, has a peculiar antero-laterally directed process, and a broad space between this and the clavicles which may have been occupied by a precoracoid. Still others had a small
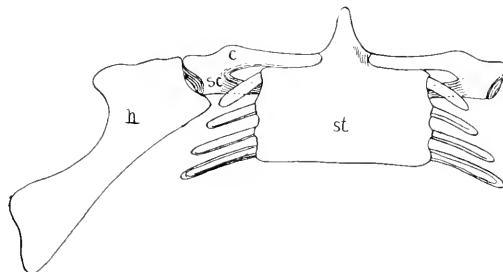
FIG. 270.—Pectoral girdle and sternum of *Ornithostoma* (Williston, '97). *c*, caracoid; *h*, humerus; *sc*, scapula; *st*, sternum.

precoracoid reaching a triangular episternum and fused laterally with the scapula. The clavicles connect by suture with the scapula.

DINOSAURIA have a large scapula, strong and usually elongate, and often connected or even fused with the small coracoid plate which is rounded in front and has a foramen near the glenoid fossa. Apparently clavicles and precoracoids are lacking; no episternum is known and the sternum is possibly represented by a pair of ossifications, not known in Theropoda.

PTEROSAURIA usually have coracoid and scapula fused (fig. 270), the scapular part being long and slender and sometimes (*Pteranodon*) attached to the anterior vertebræ. The coracoid is slender and articulated by a synovial joint with the sternum. Clavicles are absent.

AVES.—Making allowances for modifications connected with flight, there is not much difficulty in comparing the pectoral girdle of birds with those of lizards, although some homologies are not clear. The adult girdle consists of three distinct bones on either side— scapula, coracoid and clavicle—the precoracoid being reduced and no episternum present. The glenoid fossa is formed entirely by coracoid and scapula.

The scapula, which lacks a spine, is long and slender (its dorsal end expanded in penguins) and is placed differently in Ratites
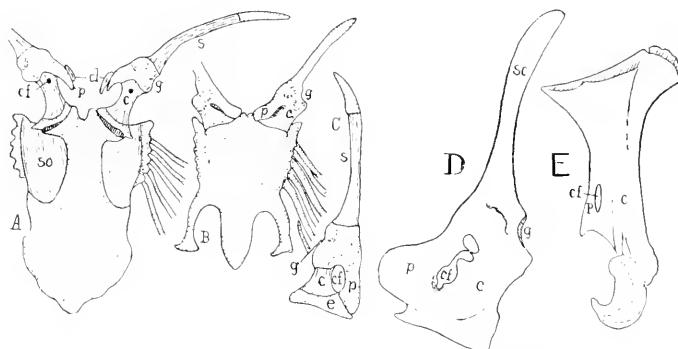
FIG. 271.—Pectoral girdles and sterna of birds. *A*, *Casuarius* (Parker, '68); *B*, *C*, young *Struthio camelus* (Parker); *D*, adult *S. australis*; *E*, *Haliætus leucocephala* (Shufeldt, '09). *c*, coracoid; *cf*, coracoid fenestra; *cl*, clavicle; *e*, epicoracoid; *g*, glenoid fossa; *p*, precoracoid; *so*, sternal ossification; *s*, scapula; cartilage stippled.

and Carinates. In both it is dorsal to the ribs, running back parallel to the vertebræ in Carinates, ascending upwards and backwards in Ratites, where the distal end is near the spinal column. It usually has a considerable acromial process on the inner ventral end which articulates with the upper end of the clavicle, the coracoid connecting with its external side. It is the most frequently pneumatic of any of the girdle bones, the opening being near the proximal end.

Although the coracoid is reduced in Ratites and fused in a straight line with the scapula in *Struthio* (fig. 271, *C*, *D*), it is primitive in its width and in having a gap which partially separates an anterior bar (fig. 271, *C*), the precoracoid. In other birds (Raptores, figure 271, *E*) the fenestra is reduced to a foramen while in other Ratites (*Casuarius*,

figure 271, *A*, *Dromœus*, *Apteryx*) the fenestra is a gap and the precoracoid is a process extending forwards and inwards from the glenoid region. The same process, in various stages of reduction, occurs in many Carinates. The Carinates are more primitive than Ratites in that the scapula and pillar-like coracoid meet at an angle, the coracoid extending to the sternum, thus acting as a brace against the action of the pectoral muscles. Carinates also have a considerable acrocoracoid process (scarcely recognizable in Ratites) beginning as a crest on the ventral side of the coracoid and extending from the glenoid region to support the broad upper end of the clavicle.

Most Carinates have the clavicles at some distance from the coracoids, except at the upper ends. These bones are long and slender, their strength and curvature parallel with the powers of flight, the extreme occurring in the diurnal Raptores. The two clavicula are fused at their ventral ends, forming the **furcula** ('wishbone'), the place of fusion having a median discoid process in Oscines and Gallinæ. The upper ends of the furcula articulate with the acrocoracoid process and (a few Carinates excepted) with the acromion of the scapula. In all Ratites (fig. 271, *A*) and some Carinates (pigeons, humming birds) the clavicles are more or less reduced, so far in some parrots and *Dromœus* that only a small rudiment rests against the acrocoracoid, while in other parrots and Ratites it is lost. Even when better developed, the fused ends do not usually meet the sternum, but are connected with it by ligament (fused with the carina in Steganopods).

It is stated that part of the clavicle is laid down in cartilage, but this needs confirmation. There is also said to be a cartilage at the junction of the two halves of the furcula, regarded by some as traces of an episternum, otherwise absent from birds, but the cartilage renders such homology doubtful.

MAMMALIA show varying degrees of mobility between the bones of the pectoral girdle, which, as a whole, presents two different conditions, the more primitive in Monotremes (figure 273, where relations are much as in Lacertilia and especially in Therapsida), the other in Placentalia; fetal Marsupials (fig. 275) are intermediate, although the adults are more like Placentals. In all the scapula is broad above, narrow at the glenoid end, and bears a separate suprascapula only in Monotremes and some Ungulates. It has a strong ridge (**spina**) on the outer surface for greater muscular attachment, dividing the surface into two fossæ, and terminating in a ventral

process, the **acromion,** with which, when functional, the clavicle articulates. Nothing certain is known of an episternum, except in Monotremes (fig. 273).

MONOTREMES, in their early stages, have either half of the coracoscapular cartilage a continuum, with a marked incisure on the
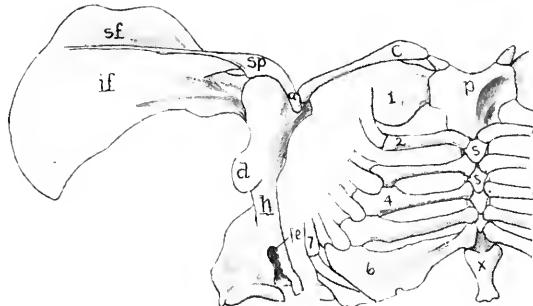
FIG. 272.—Pectoral girdle and sternum of *Tatusia* (Weber, '04). *a,* acromion; *c,* clavicle; *d,* deltoid ridge; *fe,* entepicondylar foramen; *h,* humerus; *if,* infraspinous fossa; *p,* presternum; *sf,* supraspinous fossa; *sp,* spina of scapula; *x,* xiphisternum.

anterior border, possibly homologous with one of the lacertilian fenestræ. The cartilages of the two sides meet in the middle line. Three bones ossify in each half—scapula, coracoid and precoracoid (epicora-
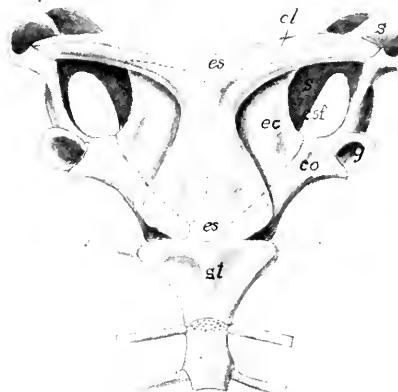
FIG. 273.—Pectoral girdle of *Ornithorhynchus*. *cl,* clavicle; *co,* coracoid; *csf,* coraco-scapular fenestra; *ec,* precoracoid; *es,* episternum; *g,* glenoid fossa; *s,* scapula; *st,* sternum.

coid of authors, see p. 229; figures 273, 274), the precoracoid ossifying later than the others and retaining a cartilage (?epicoracoid) on its medial margin. Coracoid and scapula fuse early, but the precoracoid is permanently separate and functional, the only case in mam-

17

mals.   The curved scapula of the adult is relatively narrow, has a
short spine or none, and bears a short acromion bent ventrally on its
anterior margin.   The clavicles of the two sides meet in the young;
in the adult their median ends are separate and each is closely
appressed to, and in adults fused with the transverse arms of the
episternum, which, in turn, fuses with the more dorsal sternum.

MARSUPIALIA.—In embryo Marsupials (fig. 275)ʲ the coracoid
part of the cartilage girdle abuts on the presternum, but is relatively
much shorter than in Monotremes.   This connexion is lost in the
adult and the whole is much as in Placentalia, the coracoid being
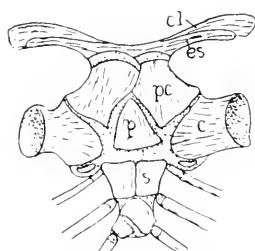
FIG. 274.—Dorsal side of sternum and
pectoral girdle of *Echidna* (Parker, '68).
c, coracoid; *cl*, clavicle; *es*, episternum;
p, presternum; *s*, sternebræ.
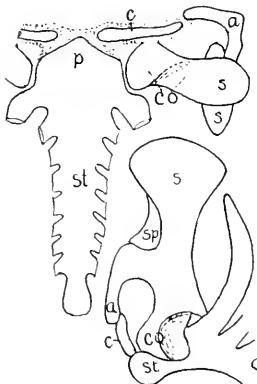
FIG. 275.—Pectoral girdle and sternum
of *Dasyurus* from pouch (Broom, '02).
a, acromion; *c*, clavicle in undifferentiated
tissue; *co*, coracoid; *p*, presternum; *s*,
scapula; *sp*, spina; *st*, sternum.

small and somewhat hooked.   The clavicle (none in bandicoots)
extends from acromion to sternum, 'omosternal' cartilages inter-
vening.   It is not always completely ossified.   No episternum occurs.

PLACENTALIA have the ventral parts of the girdle greatly
reduced, reduction sometimes extending to complete loss of the clavi-
cle, while the coracoidal parts are a small coracoid process fused
usually with the lower end of the scapula.   The scapula is well
developed, is usually triangular (sometimes quadrangular) in
outline, and is plate-like, with a strong spine terminating in an acro-
mion except in whales.   The acromion bends ventrally, often extend-
ing beyond the shallow glenoid fossa, and articulates with the clavicle
when the latter is present.   The spina is close to the anterior margin
in lower mammals, in the higher the prespinous part is increased so

that the spine may be nearly median, separating two fossæ for muscles.
Many Edentates (fig. 272), Insectivores and Carnivores have a second
crest on the same surface. In swine the line between scapula and
suprascapula is pierced by foramina for the dorsal rami of spinal
nerves. The coracoid process is a small projection on the medial side
of the glenoid fossa and in the adult is fused with the scapula, as is
the coracoid in many lower Vertebrates. *Myrmecophaga* has a bar
from the process to the anterior margin of the scapula, enclosing a
foramen.

The coracoid process arises from two centres in many mammals (Edentates,
Ungulates, Rodents, Sirenia, Carnivores and Primates) and for a time after birth
the two coracoidal bones retain
their individuality (fig. 276), the
anterior being excluded from the
glenoid fossa. Reference to these
two elements is made on page 245.

FIG. 276.—Proximal end of scapula (s) and
coracoidal bones of 7 weeks *Lepus* (A), and (B)
young *Bradypus* (Howes, '93). c^1, anterior
coracoid, forming greater part of human cora-
coid; c^2, posterior coracoid (metacoracoid); f,
coraco-scapular fenestra; l, ligament.

The extent of develop-
ment of the clavicle is related
to the amount of freedom of
motion of the fore limb, and
is greatest where there is a
variety of motion as in bats, climbing mammals and man. There is
a tendency towards loss where only a pendulum motion occurs as
in walking or swimming (Ungulates, whales, Sirenia and individuals
of other orders). Between full development and complete loss
are varying conditions (armadillos, Carnivores, etc.). When best
developed the clavicle forms a brace between shoulder blade and
sternum. Moles have a cuboidal clavicle, described as partly
cartilage, partly membrane in origin, and similar origin is stated
for other genera, so that in these it may be a composite bone as in
Anura, or it may be that the cartilage has no such morphological
significance.

A pair of cartilages may intervene between the clavicles and the anterior end
of the sternum, often ossifying as separate bones which have been called remnants
of precoracoids, presterna, preclavia and omosternum, a variety of names indicat-
ing the uncertainty as to their morphology.

INSECTIVORA have a long and narrow scapula, with spine and acromion
little developed in moles, the acromion bifurcate in shrews, one ramus articu-
lating with the clavicle. Other Insectivores have a more typical scapula. The
clavicle (possibly a compound bone) is usually present and in Talpids articulates

with the humerus (not paralleled elsewhere in mammals) and with the prester-
num.   Talpids also have short and quadrangular clavicles and humeri: elsewhere
the clavicle is long and slender.

CHIROPTERA (fig. 277) have a large oval scapula, the spine near the anterior
border, with one or two small ridges (accessory spinæ) behind it, the spine itself
being short and rather high.   The acromion is large and the long curved coracoid
is sometimes forked at the tip.   The strong clavicle extends from sternum to
scapula, making a strong brace against the action of the large pectoral muscles.

EDENTATA.—The pectoral girdle of Edentates varies considerably.   In the
Tubulidentata the scapula is normal, the clavicle strong and curved, and has
the ventral end expanded.   Pholidota have a broad scapula, rounded dorsally,
with a suprascapular cartilage, and a spine rather nearer the posterior than the
anterior border.   The acromion is small,
the coracoid greatly reduced and no
clavicle is present.   Xenarthra (fig. 278)
have a broad scapula, often with an
accessory spine, an acromion, slender in
Myrmecophaga, long and curved in arma-
dillos, and often with a facet on the
inner surface for the humerus: in sloths
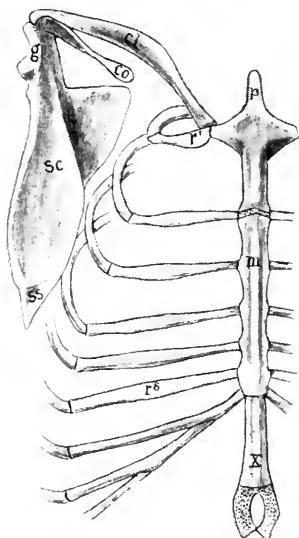
FIG. 277.—Pectoral girdle, ribs and
sternum of *Eumops californicus*. *cl*,
clavicle; *co*, coracoid; *g*, glenoid fossa;
m, mesosternum; *p*, presternum; *r*,
ribs; *sc*, scapula; *ss*, suprascapula; *x*,
xiphisternum.
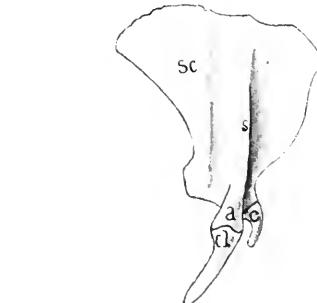
FIG. 278.—Scapula of *Dasypus 6-cinctus*.
a, acromion; *co*, coracoid; *cl*, clavicle; *s*,
spina; *sc*, scapula.

the spine rises only from the ventral part of the scapula, and there is no second-
ary spine.   Many Xenarthra have a marked incisure in the anterior border of the
scapula just dorsal to the coracoid, which is converted into a coraco-scapular
foramen in *Myrmecophaga* and sloths by the union of the precoracoid part of the
process with the anterior border of the scapula.   The clavicle is small or absent
in anteaters, well developed in armadillos and the two-toed sloth, reduced in
other sloths.

RODENTIA usually have a long slender scapula with a long acromion (espe-
cially long in *Myopotamus*).   The coracoid is always small and the clavicle varies

from well-developed to absent; when small it is often enclosed in ligament; its connexion with the sternum varies accordingly.

CARNIVORA have the scapular spine at about the middle of the bone, except in Otariidæ where it is nearer the posterior border; it is always well developed as is the acromion. The coracoid is small, the clavicle reduced or absent; when best developed (Felidæ) it does not reach scapula or sternum; it is absent in Pinnipeds and most bears.

CETACEA have a very broad and flat scapula in most Odontocetes, less broad in Mystacocetes. The spine is reduced, the acromion has a narrow base and is parallel to the coracoid, both being reduced in *Megaptera*. None of the whales have a clavicle.

UNGULATA.—All Ungulates have a long and rather narrows capula, the suprascapula being imperfectly ossified in most Artiodactyls, swine having a number of foramina for the dorsal rami of the spinal nerves in the line between the two elements. The acromion is distinct in most Artiodactyla, but is lacking in giraffes. In Perissodactyla the spine inclines backwards and there is no acromion, while the coracoid is short and blunt. No modern Ungulates have a clavicle, but a transitory one is reported in the sheep embryo.

HYRACOIDEA have a small triangular scapula with a small spine but no acromion. The dorsal part of the scapula persists as a suprascapular cartilage. No clavicle occurs.

PROBOSCIDIA have the scapula with a curved dorsal border and a large spine near the anterior margin, this ending in an acromion with a posterior process. The coracoid is small and rounded and no clavicle occurs.

SIRENIA have a scapula much like that of seals, narrow and curved behind, and with the spina moderate and near the middle of the bone. The acromion is slender, pointing downwards. No clavicle present.

PRIMATES.—The scapula of the lower primates is narrow, that of the Anthropoids is broad, with the spine near the anterior margin. Both acromion and coracoid process are large, the latter often somewhat hooked. The well developed clavicles are connected with both scapula and sternum.

PELVIC GIRDLE

The Tetrapodan pelvis differs from that of fishes in being connected with the vertebral column by the intervention of sacral ribs (p. 25). This connexion is the result of the terrestrial habitat and the need of a firmer support of the body on the legs, since it is no longer buoyed up by the water. There is less uncertainty as to the homology of parts in different groups than in the case of the pectoral girdle, but some questions are not yet solved. In the procartilage stage the two halves of the girdle are separate as in fishes, and only with chondrification are the three elements differentiated. These are an ilium dorsal to the acetabulum, below it an anterior os pubis and a posterior ischium, all of which usually ossify, as sometimes

does a fourth bone, the acetabular.   All three meet as a rule in the acetabulum which is cup-shaped, but occasionally the pubis is excluded, the cup then being formed by ilium and ischium, the acetabular bone sometimes participating.   The ilium is connected with the vertebral column in all cases where the development is known, by sacral ribs, the connexion varying in firmness, being effected by ligament, cartilage, or actual fusion.   Usually the pubes and ischia of the two sides meet below in a median symphysis, the ischia failing to meet more often than the pubes.   Occasionally all sym-physial sutures and those of the acetabular region are obliterated in the adult.

AMPHIBIA.—The Aistopod Stegocephals, Gymnophiona and *Siren* lack a pelvis; the Anuran pelvis is greatly modified in correla-tion with the leaping habits.

STEGOCEPHALA (fig. 279) have only the bones preserved, but their distances from each other and their relations are such as to warrant the conclusion that

there was a large amount of cartilage present which has left no trace.   All three elements are ossified in part, and the pair of ischia, larger than the pubes, are frequently united in a sym-physis.   The short and stout ilium is connected with the single sacral vertebra.
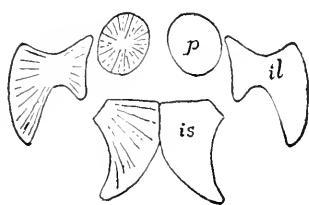
FIG. 279.—Pelvis of *Disco-saurus* (Credner). *il*, ilium; *is*, ischium; *p*, pubis.

URODELA.—In these Amphibia the cartilages of the two sides grow around the obturator nerve and fuse in the middle line, forming a large ischio-pubic plate with the obturator foramen in front of the acetabulum.   Later, there is an ischiadic ossification on either side (none in *Proteus*), the rest of the plate persisting as carti-lage.   The anterior end of the plate is often prolonged as an epipubic process (fig. 280), and in lunged Salamandrina this is replaced by an independent ypsiloid cartilage (fig. 281), divided at the tip, which affords origin for respiratory muscles.   Its homology with the epipubis is not certain.   It arises apart from the pubic cartilage and develops later than the other pelvic cartilages.   The ilium is always short, is more or less ossified and is connected with a single sacral vertebra by ligament or direct articulation, its upper end often persisting as cartilage.

ANURA have a pelvis (fig. 282) differing greatly in form from that of Urodeles.   In the early stages the halves of the ischio-pubic

cartilage do not surround, but lie in front of the obturator nerve so that no foramen is formed. Occasionally there is an ossification of an os pubis (Aglossa). A third difference is the great elongation of the ilium which connects with a single sacral vertebra (in one or two
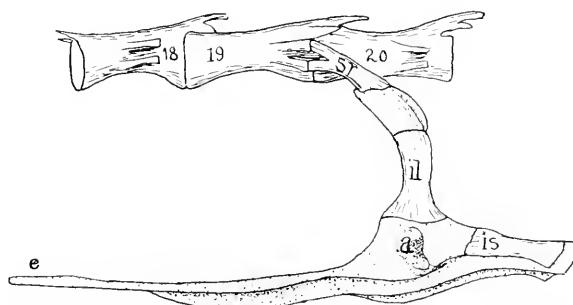
Fig. 280.—Pelvis of *Necturus* (Wilder, '03). *a*, acetabulum; *e*, epipubis; *il*, ilium; *is*, ischium; *sr*, sacral rib; 18–20, vertebræ. Bones lined, cartilage stippled.

fossils two sacrals are described). The acetabulum is a cup, bounded by ossified ischium and ilium, a cartilage (probably pubic) lying on its lower anterior side. The acetabular region is very short, laterally compressed, and forms a plate in the median line, the two acetabula being separated by cartilage. In Aglossa the two sides are distinct, the region less compressed and, besides a pubis, an epipubis is present.
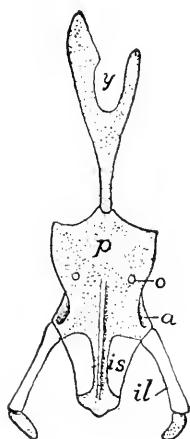
Fig. 281.

Fig. 282.

Fig. 281.—Pelvis (ventral side) of *Cryptobranchus* (Wiedersheim). *a*, acetabulum; *il*, ilium; *is*, ischium; *o*, obturator foramen; *p*, pubic cartilage; *y*, ypsiloid cartilage.
Fig. 282.—Pelvis of frog. *a*, acetabulum; *il*, ilium; *is*, ischium; *p*, pubic? cartilage.
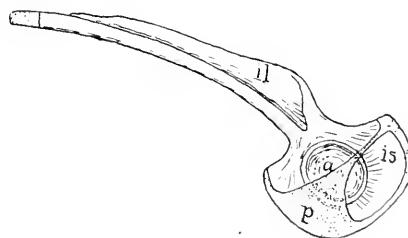
REPTILIA.—Where development is known, the reptilian pelvis arises from a pair of cartilages, each with a large gap on the

median ventral side, partially separating pubic and ischiadic parts. This gap persists in the adult, and when the halves meet in the ventral symphysis, the gaps become ischio-pubic fenestræ, usually separated by ligament, rarely (Chelonia) by cartilage or bone in the middle line from ischium to pubis. This median cartilage may extend through the symphysis and in front of the pubes as an **epipubis (epigastroid)**, behind the ischia as a **hypoischium (hypogastroid)**. These median parts may remain cartilage or may ossify as independent bones, the hypoischium sometimes being called an **os cloacæ** when it becomes involved in the cloacal wall.

The term os cloacæ is also given to paired bones in the wall of the cloaca of a few lizards; nothing is known of their history but they are evidently not the same as the hypoischium (fig. 284).
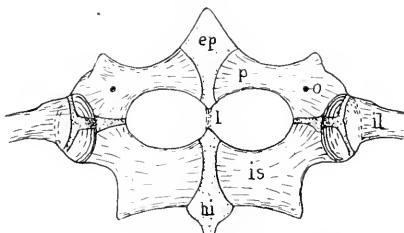
FIG. 283.—Pelvis of 23 cm. *Sphenodon* (Schauinsland, '03). *e*, epipubis; *hi*, hypoischium; *il*, ilium; *is*, ischium; *l*, pubo-ischiadic ligament; *o*, obturator foramen; *p*, pubis.
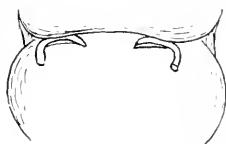
FIG. 284.—Os cloacæ of *Gonatodes* (Noble, '21).

Many fossil reptiles lack the ischio-pubic fenestra, pubis and ischium of the same side meeting in a continuous line. In others, as in Stegocephals, the ossifications are small, the cartilages apparently having been much larger, and in these the presence or absence of fenestræ cannot be decided. In some groups (Squamata, Rhynchocephala) there is a separate obturator foramen in each pubis, but in most modern orders the obturator nerve passes through the fenestra as in mammals. Which condition is the more primitive is uncertain. Amphibia throw no light on the matter as the living species have no ischio-pubic fenestra.

Except in Dinosaurs, the ilium is smaller, as a rule, than the other pelvic bones, and is usually connected with two sacral vertebræ, the exceptions among living species being snakes, and some apodal lizards in which the pelvis is reduced or absent, while in Ichthyosaurs and some Pythonomorphs the reduced pelvis and vertebral

column are not connected. Usually ischium and ilium meet in the acetabulum which usually is a closed cup with imperforate bottom.

SQUAMATA.—Except in the apodal forms, the pubis, transverse at first, changes its direction during development, so that it extends
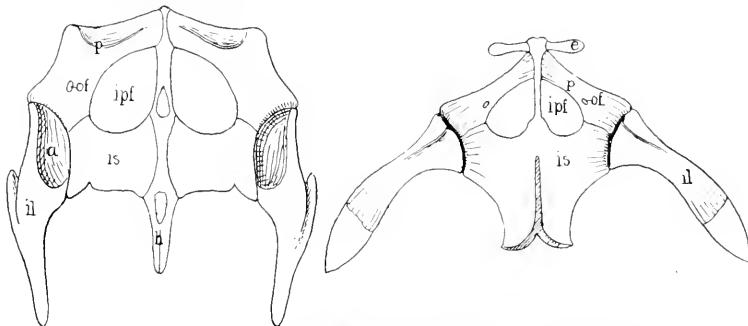
FIG. 285.—Lacertilian pelves: *A*, *Monotor bivittatus; B, Chameleo* Hoffmann, '90). *e*, epipubis? *h*, hypoischium; *il*, ilium; *ipf*, ischio-pubic fenestra; *is*, ischium; *of*, obturator foramen; *p*, pubis; *a*, acetabulum;

obliquely forwards and inwards (fig. 285), thus enlarging the fenestra. Except in *Chameleo*, where it is nearly vertical, the ilium extends downwards and forwards from the sacrum, with which it is movably connected by cartilage and sacral ribs, a part dorsal to the connexion often persisting as cartilage. Usually cartilage persists in the ischiopubic symphyses and may extend from the pubes nearly to the ischia, partly separating the fenestræ. The ischiadic cartilage is more frequently ossified. There is usually a marked epipubis (sometimes paired) occasionally ossified (in *Chameleo*, figure 285 *B*, as two small rods). The hypoischium, usually movable, is well developed and may be carti-lage or bone in the adult. Many lizards have prepubic processes extend-ing forwards and either inwards or outwards. At times they are well-

FIG. 286.—Pelves of apodal Squamates: *A, B, Seps; C, Ophi-saurus* (lizards); *D, Cylindrophis* (Fürbringer, '70). *f*, femur; *i*, iliopectineal; *il*, ilium; *ip*, ischio-pubis; *p*, pubis; *t*, tibia.

developed, at others scarcely more than knobs on the antero-lateral border of the pubes. All three pelvic bones meet in the imperforate acetabulum.

Apodal lizards have the pelvis reduced (fig. 286, *A-C*), sometimes to all but complete loss. Some (*Bipes. Ophisaurus, Anguis*) have the two separate halves of the reduced pelvis attached to the sacrum, all three bones (sometimes fused) being recognizable.

Most Ophidia have lost all traces of hind limbs and girdles, but a few (*Tortrix, Typhlops*, etc.) have isolated bones in the pelvic region (fig. 286, *D*). These are better developed in some of the larger species (*Python, Boa*) where all three bones occur, as well as bones of the free limbs.

The pelvic girdle of Pythonomorphs is lacertilian in type, but reduced in correlation with the loss of supporting function of the hind limbs.

CHELONIA.—Like the pectoral, the pelvic girdle of turtles is within the bony case, with which it is connected by ligaments or is
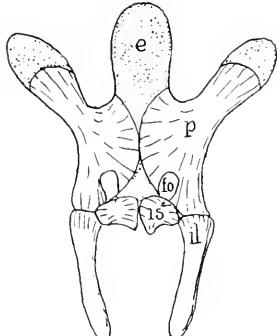
FIG. 287.—Pelvis of *Sphargis* Hoffmann, '90. *e*, epipubis; *fo*, obturator foramen; *il*, ilium; *is*, ischium; *p*, pubis; cartilage stippled.
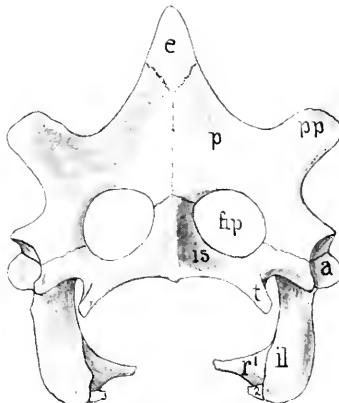
FIG. 288.—Pelvis of *Chelydra* from below. *a*, acetabulum; *e*, epipubis; *fip*, ischiopubic fenestra; *il*, ilium; *is*, ischium; *p*, pubis; *pp*, prepubis; *r*, sacral tibs; *t*, tuber.

more firmly united. All three bones meet in the acetabulum and the obturator nerve passes through the ischio-pubic fenestra. The long ilium runs ventrally and forwards, its dorsal attachment differing in different groups. In Cryptodires it is attached to the sacral vertebræ and the eighth costal plate; in *Trionyx* and its allies to the sacral ribs only, and in all Pleurodires to the carapace and not to the sacral ribs.

Pubis and ischium are nearly parallel to the plastron, the bones of the two sides meeting in the middle line. Pubes and ischia are connected by ligament in Trionychidæ and marine turtles (fig. 287); in land and fresh water species by cartilage or bone (fig. 288), these medial structures separating the fenestræ of the two sides. Pre-

pubic processes (either long rods, or plate-like with expanded ends), extending outwards and forwards, are common. An epipubis (paired in origin and usually persisting as cartilage) is frequently present. A hypoischium appears in development, but is lost later. All Cryptodires have a lateral process (**postischium**) on the hinder side of each ischium.

CROCODILIA differ from other recent reptiles in the exclusion of the pubis from the acetabulum, unless it be that the cartilage (fig. 289) which connects the bone with the pelvis be its basal part. In the earliest crocodile-like rep-
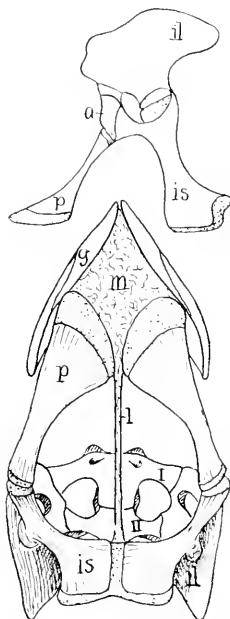
FIG. 289.—Side and ventral views of pelvis of *Alligator* (Wiedersheim). *a*, acetabular cartilage; *g*, last gastrale; *l*, ligament; *m*, membrane between *p*, pubis and gastralia.
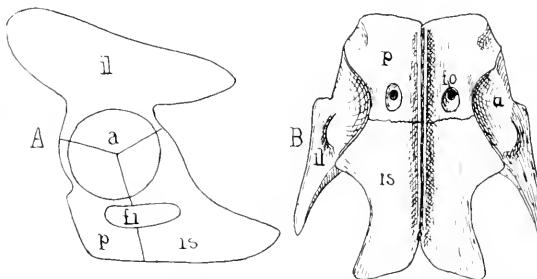
FIG. 290.—Pelves of Theromorphs: *A*, *Diademon* (Broom, '95); *B*, *Limnoscelis* (Williston, '11). *a*, acetabulum; *fi*, ischio-pubic fenestra; *fo*, obturator foramen; *il*, ilium; *is*, ischium; *p*, pubis.

tiles, the Pseudosuchia, the os pubis forms part of the acetabular wall. Another crocodilian peculiarity is the perforation of the acetabulum. The ilium, inclined downwards and forwards, is expanded dorsally and articulates with a pair of sacral ribs. The long pubes do not meet, but are connected by a strong membrane which extends from the pelvis to the gastralia. The ischia are strong and meet in a cartilaginous symphysis; each sends an anterior process forwards which bounds the acetabulum below.

THEROMORPHA (fig. 290).—The pelvis of these reptiles is primitive in many respects. The ventral bones show less variety than does the ilium. The latter may be rather long and tapering (*Dicynodon*) recalling the Anura, or it may expand dorsally into a crest extending the length of several vertebræ. The ilium may be vertical, or inclined forwards or backwards. The crest extends

backwards in Pelycosaurs, forwards in many Therapsids, where it may be very large.   Pubis and ischium are usually plate-like; some are imperforate, some have an obturator foramen in the pubis; in others it is merged in the fenestra. Some have ischium and pubis suturally connected, sometimes the sutures are obliterated.   The acetabulum may be open or closed.

ICHTHYOSAURIA, with the reduced use of the hind limbs, have a simplified pelvis which has lost the connexion with the vertebral column and was embedded in the muscles.   All three bones apparently met in the acetabulum and are not closely united with each other.   All are slender, the ilium directed downwards and forwards, the ischium smaller than the pubis.

SAUROPTERYGIA have a stronger pelvis, the bones often loosely united.   Some have a long and slender ilium, others have it large and stout and often fused with the ischium, both bones being nearly flat.   The ventral elements remain largely cartilage, the pubis being at least as large as the ischium.   Fenestra and obturator foramen are united, the foramen sometimes being indicated by a notch on the posterior border of the pubis.   Both pubis and ischium are
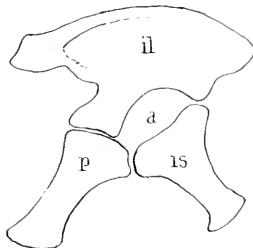
FIG. 291.—Pelvis of *Brontosaurus* (Marsh). *a*, acetabulum; *il*, ilium; *is*, ischium; *p*, pubis.
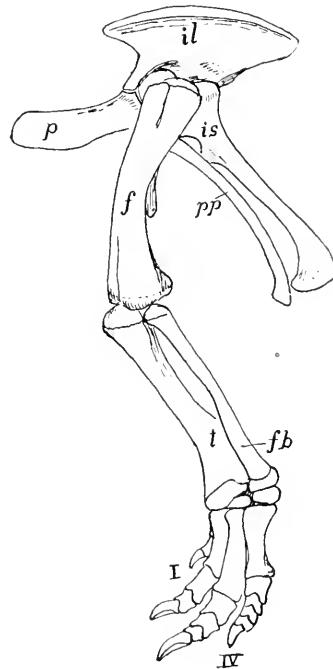
FIG. 292.—Pelvis and hind leg of *Camptosaurus* (Marsh). *f*, femur; *fb*, fibula; *il*, ilium; *p*, pubis; *pp*, post-pubis; *t*, tibia; I–IV, digits.

thickened near the acetabulum of which they form a part.   Pubes and ischia of the two sides either meet directly or with cartilage between them.

DINOSAURIA have all three bones meeting in the usually perforate acetabulum.   The long ilium is connected with the sacral and synsacral vertebræ, the synsacrum containing a number of bones correlated to some extent with the character of locomotion.   The ventral bones differ in the two sub-orders.   In both there is no prepubis, the ischium is long and slender.   Saurischia (figure 291, closest to other reptiles) have a triradiate pelvis; pubes and ischia have a ventral (often long) symphysis, and in some the pubis, directed forwards, has a small preacetabular process and no postpubis.   The ischium is long and slender,

extending backwards and downwards. Ornithischia (fig. 202) have a quadri-radiate pelvis; the pubes do not meet in the middle line and lack a prepubis, but have a ventral **postpubis** extending from beneath the acetabulum downwards and backwards paralleling the long and slender ischium which bears an obturator process.

At first sight the Ornithischian pelvis resembles that of birds, and some would recognize exact homologies between the two groups. Others hold, on the grounds of ontogeny, that the avian pubis is at first directed forwards and only later comes to parallel the ischium (p. 270), giving off, in the adult, a (pectineal) process which simulates the pubis of the Ornithischian Dinosaur.

PTEROSAURIA have an elongate pelvis (fig. 293), the preacetabular part being the longer. Ilium and ischium are fused, excluding the pubis from the acetabulum. The pubis apparently was loosely attached to the other bones, its distal end expanded in some species; while in some the pubes of the two sides met in the mid-ventral line.

FIG. 293.—Pelvis of *Pterodactylus* (Zittel). *il*, ilium; *is*, ischium; *p*, pubis.

AVES.—As stated above, in spite of very marked superficial similarities, the pelves of birds and Ornithischia are structurally very different, the apparent similarities being doubtless to be explained on the grounds of similarity of posture, these reptiles, like the birds,
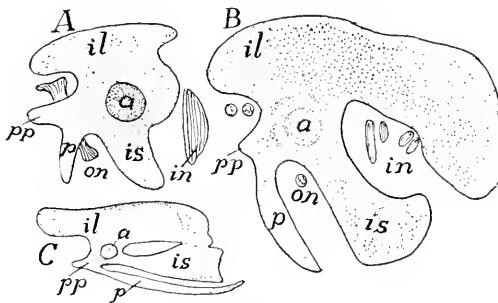
FIG. 294.—Development of pelvis of chick (Miss Johnson, '83). *A*, 6-day chick; *B*, older; *C*, 20 days. Cartilage stippled; bone white. *a*, acetabulum; *il*, ilium; *in*, ischiadic nerve; *is*, ischium; *on*, obturator nerve; *p*, pubis; *pp*, pectineal process.

being largely bipedal. The early stages of the avian pelvis (fig. 294) have parts resembling those of embryo lizards, ischium and pubis pointing towards the median plane, and having a deep incisure between them in which is the obturator nerve, while the pubis has a marked

prepubic process. Later, the pubis gradually turns posteriorly, finally paralleling the ischium, thus coming to a position similar to that of the Ornithischian postpubis, the pubis of the latter resembling the prepubic process of many birds (fig. 295).

In adult birds the bipedal posture demands a strong connexion of pelvis and vertebral column, since the pelvis lies behind the centre of gravity of the animal. Hence there is a great elongation of the ilium, forwards and back, and its fixation to many more than the primitive two sacrals, the result being the synsacrum (p. 48), in which a varying number of vertebræ have united with the true sacrum, and the ilia of the two sides have fused with these. The union of pelvis and synsacrum is strengthened by the meeting of the ilia of the two sides (sometimes for their whole length) dorsal
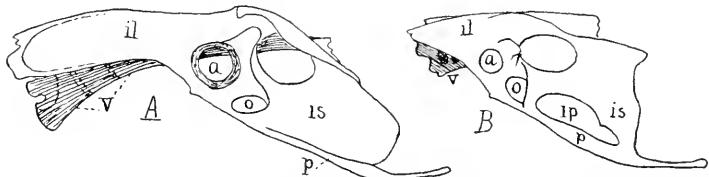
Fig. 295.—Pelves of (*A*) *Polyborus* (Shufeldt, '09) and (*B*) *Picus pileatus.* *a*, acetabulum; *il*, ilium; *ip*, ischio-pubic fenestra; *is*, ischium; *o*, obturator foramen; *p*, pubis; *v*, vertebræ.

to the vertebræ, and their fusion with the spinous processes and sometimes with the transverse processes of the synsacral vertebræ, the spaces between ilia and vertebræ often being more or less occupied with bone. Usually the ilium is concave externally in front and more convex behind, and it is most frequently pneumatic of any of the pelvic bones. The acetabulum, always open, is near the middle of the ventral margin of the ilium which sends down pre- and postacetabular processes which fuse (except in *Archæopteryx*) with pubis and ischium respectively, forming anterior and posterior acetabular walls.

Pubis and ischium are directed backwards and are relatively more slender than in other groups, some Dinosaurs excepted. Both are nearly parallel with the lower border of the ilium, the pubis being usually the longer of the two. As a rule there is no symphysis of either, the pelvis, except in *Struthio*, being widely open below. Usually ischium and ilium are fused at both ends, enclosing an ilio-schiadic fenestra. Primitively ischium and pubis are separate, but

often a process from the ischium fuses with the anterior part of the pubis, bounding an obturator foramen (fig. 295, *A*), and behind this another process from the ischium may approach and even fuse with the posterior part of the pubis (fig. 295, *B*) enclosing an ischio-pubic fenestra.

The short ilium of *Archæopteryx* is not fused with the true sacrals. The four anterior synsacrals of penguins are fused and connected by ligament only with the ilium, while a prepubic process arises some distance in front of the acetabulum. The anterior part of the ilium is the longer in Raptores (fig. 295, *A*) and the pubis is greatly reduced, scarcely extending behind the obturator foramen.
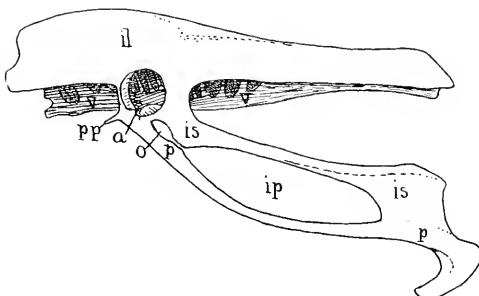
Fig. 296.—Pelvis of *Struthio.* *a*, acetabulum; *il*, ilium; *is*, ischium; *o*, obturator part of *ip*, ischio-pubic fenestra; *p*, pubis; *pp*, prepubic process; *v*, vertebral column.

Ratites show several primitive characters. *Struthio* has a pubic symphysis, and except in *Rhea* and *Dromæus*, the hinder end of the ischium is free from the ilium. The two ilia of *Rhea* fuse ventral to the posterior end of the synsacrum. Prepubic processes are usually well developed, but in adult Carinates are often lacking, although present in the embryo.

MAMMALIA.—A pelvis occurs in all mammals and is well developed except in Cetacea and Sirenia. In all, except these two orders, it is composed of the three bones (an acetabular bone is also often present), those of each side fusing early, except in Monotremes, to an **innominate bone.** Usually the two innominates are not fused in the mid-ventral line, and they may even fail to meet (many Insectivores, etc.).

In ontogeny the procartilage of either side has three radiating processes, iliac, ischiadic and pubic, the obturator nerve passing between pubis and ischium. Later, a process from the distal end of the ischium (fig. 297) meets and fuses with the distal end of the pubis, closing the ischio-pubic fenestra (obturator foramen of human

anatomy), the medial boundary of the fenestra being osseous in the adult, a condition paralleled in recent reptiles only in Chelonia. Three (or four) centres of ossification occur in the cartilage, and in many species all three bones enter the acetabulum, which is imperforate, except in Monotremes, where the acetabular cup has a complete boundary wall. In other groups the wall has a gap between ischiadic and pubic parts for the round ligament (l. teres) connecting the head of the femur with the bottom of the cup.

The adult pelvis differs from that of most reptiles and resembles that of Therapsida and Amphibia in the ventral and posterior direc-

tion of the ilium from its connexion with the sacrum, and this general direction is repeated in ischium and pubis, the latter the least inclined of the three, while the ischium often appears as a direct continuation of the ilium (fig. 300). In the more primitive orders (Marsupials, Ungulates, most Rodents) both pubis and ischia are connected in the middle line by symphysis, an interpubic cartilage intervening in some Insectivores, Edentates and bats, recalling the epipubis of non-mammals. More commonly there is no ischiadic symphysis, and in many bats, Soricidæ and Talpidæ (fig. 299) even the pubes are connected only by ligament, lost in the prepared skeleton.

FIG. 297.—Early stages of pelvis of sheep (Mehnert). *il*, ilium; *is*, ischium; *p*, pubis.

Primitively the ilium is long and slender and not infrequently is prolonged in front of the sacral articulation—the union of the ilium with one or two sacral ribs of the true sacrals, and by cartilage or ankylosis (some bats and Edentates), with the synsacrals. The chief iliac modifications are the development of a crest on the dorsal margin (large in Edentates) and sometimes a lateral crest parallel to the axis, which in primitive forms ends in a posterior ventral spine.

The ischium is usually larger than the pubis with which it is connected on either side of the fenestra. The ischia are rarely (some Edentates and bats) connected with the vertebral column, their upper margins then uniting with several postsacral vertebræ. Occasionally a process like a postischium is present, and there may be strong ischiadic tuberosities on the posterior border of the bone. The pubes are directed downwards and more or less backwards. They are parallel or may diverge behind in bats and some Insectivores, and some genera of several orders (Marsupials, Rodents, etc.) have a

well-developed **prepubic (ilio-pectineal) process** on the anterior border of the pelvis, this sometimes arising from the ilium.

MARSUPIALS and MONOTREMES have a pair of **marsupial bones,** preformed in cartilage (persisting as such in *Thylacinus*) and movably articulated with the pubes (fig. 298); they are about equally developed in the two sexes. Their ontogeny is imperfectly known and there is uncertainty as to their homologies. They are contradictorily stated to arise independently in the linea alba, and from the pubic cartilages. They have been compared with prepubic processes, with epipubic structures (paired in some reptiles, and with the Urodelan ypsiloid cartilage. They are relatively larger in Monotremes than in Marsupials, although the marsupium is less developed in the former order. No similar structures occur in Placentals, unless it be the paired (*Manis, Pteropus*) or unpaired bones (*Dasypus, Cholœpus*) in the symphysial cartilage.

FIG. 298.—Pelvis of *Ornithorhynchus. a*, acetabulum; *il*, ilium; *is*, ischium; *m*, marsupial bone; *o*, obturator fenestra; *p*, pubis; *sv*, sacral vertebræ.

Most mammals (Monotremes, rodents and bats excepted) have the peculiar acetabular **(cotyloid) bone** which ossifies separately in the pelvis. In some mammals it remains discrete, but usually it fuses with ischium or ilium, excluding the pubis from the acetabulum. When it unites with the pubis, the latter appears to enter the cup, which is not the case except in Monotremes, seals and some Ungulates. The acetabulum is usually a hemispherical cup when the limb has freedom of motion, but when it swings in a single plane, the shape may be altered. The cup usually faces laterally, but in bats (fig. 301) it is more dorsal and the knee looks dorsally in adaptation to the wing membrane.

INSECTIVORA.—The Talpids (fig. 299) have a very long pelvis, all bones being long and slender, and in these and the Soricidæ there is no ventral symphysis. The symphysis is short in *Erinaceus* and restricted to the pubes which are ankylosed, while in Monotyphla both bones are concerned. The Talpids have a long and narrow obturator foramen.

CHIROPTERA have a small pelvis (fig. 300), in correlation with the slight use of the hind limbs. Except in Rhinolophidæ the halves are connected by ligament. The ilium is a rod, the pubes have a prepubic process which, in the

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Hipposiderinæ, extends to the ilium, enclosing a preacetabular foramen. The acetabulum is high on the pelvis and is directed more or less upwards.

EDENTATA.—The pelvis is short in sloths, longer in other Xenarthra, and longest in Tubulidentata. The ilia are broadest in sloths; in other forms they are broad above and narrower near the acetabulum. Except in Tubulidentata, the ischia are fused with several (five in armadillos) synsacrals, bounding a sacro-ischiadic fenestra. The symphysis is short (of the pubes only in *Oryctero-pus*) and is usually ossified. The obturator fenestra is large.

RODENTIA have the ilium short and slender, pubes and ischia flat, the pelvic bones diverging behind. The long symphysis is often ossified, an exception occurring in guinea pigs where the halves are connected by ligament.

CARNIVORA.—The pelves of the Fissipedia and Pinnipedia differ consider-ably. The former have a long and narrow pelvis, the subequal ilium and ischium being in a straight line. The ilium is usually straight and flat, narrower near the acetabulum, and expanded as a crest dorsal to the sacral articulation. The long sym-physis includes ischium and pubis and the obturator fenestra is oval. The Pinnipedia have very short ilia, the crests turned outwards; pubes and ischia are long and slender, the fenestra long and narrow. The symphysis is short, the halves slightly connected. The acetabulum lacks the incisure for the teres ligament.

FIG. 299. — Ventral view of pelvis of *Scap-anus latimànus*, showing absence of symphysis.
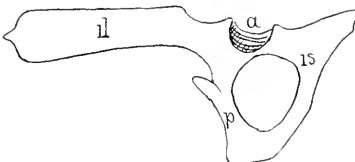
FIG. 300.—Pelvis of *Pteropus*. *a*, acetabulum; *il*, ilium; *is*, ischium; *p*, pubis.

CETACEA have a long, slender bone (?ischium) on either side of the body, this longer in the male. It is nearly parallel with the backbone and is connected with its fellow by ligament. *Balæna* has a rudimentary acetabulum and rem-nants of a femur. *Platanista* has lost the pelvis entirely.

UNGULATA have a long pelvis, the ilium expanded dorsally, narrower near the acetabulum, the dorsal crest turned outwards in Artiodactyls. Ruminants have a large preacetabular fossa. The symphysis is long in Artiodactyls, includ-ing most of the ischium, the fenestra being oval. The ischium is shorter, the fenestra nearly circular in Perissodactyls.

HYRACOIDS recall the Artiodactyls in the appearance of the small pelvis.

PROBOSCIDIA have a greatly expanded pelvis, the broad ilium being turned outwards, the acetabulum looking downwards. Pubis and ischium are small, both entering the symphysis, most of the ischium being included.

SIRENIA, in accordance with their aquatic life, have a greatly reduced pelvis. In the ancestral *Eotherium* all three bones are present, pubis and ischium bounding a fenestra; and in *Halitherium* there is a rudimentary acetabulum and femur. *Halicore* has but two bones—ilium and pubis—on either side, the former connected with the sacrum by ligament. *Manatus* has merely a single triangular bone on a side.

PRIMATES.—Most Lemurinæ and Simiæ have a wide pelvis, in other lemurs it is narrow. When wide, the pubis is broad and the symphysis is restricted to this part. An acetabular bone is common in the young, fusing in various ways in the different genera, but always excluding the pubis from the acetabulum. The old-world apes often have ischial tuberosities ending in a broad flat surface which is connected with the ischial callosities of the skin.

FREE APPENDAGES

The free appendages of Tetrapoda are very different from the fins of fishes, but no doubt exists as to their general homology, though it is difficult to trace details in the two groups, and what parts of the one are what parts of the other is uncertain. The Tetrapod appendage has to support the body weight, a necessity of the terrestrial life, and this requires, not the general flexibility of the fin, but a rigid support and also joints permitting much motion, with muscles to hold the parts firmly when occasion calls.

As in fishes, the appendages arise as paired horizontal folds, extending over several somites, and at first (especially in Amniotes) the early stage of an appendage is a paddle with narrow base and a broader end evenly rounded at first, later developing the (five) digits from the margin. Chondrification proceeds distally, except for delay in the basipodal region.

Pectoral and pelvic limbs are closely similar (homonomy), part corresponding to part almost to details. Each has a proximal segment (upper arm or **brachium,** thigh or **femur**) called the **stylopodium** (fig. 242). Next is a **zeugopodium** (forearm or **antebranchium, crus** or shank) and this is followed by the **autopodium** (hand or **manus,** foot or **pes**). There is a single stylopodial bone (**humerus** in the arm, **femur** in the leg) and two zeugopodial bones, **radius** on the preaxial side of the fore limb, **ulna** on the other, and **tibia** and **fibula** in similar positions in the hind limb.

Humerus and femur have a head, usually more or less hemispherical, which fits in the socket (glenoid fossa, acetabulum) in the girdle. Each usually has prominences near the head (**tuberosities** on the

humerus, **trochanters** on the femur) for the insertion of muscles. Usually there are two tuberosities—radial (**majus**) and ulnar (**minus**) on the humerus, the names in parentheses those of human anatomy. The femur has tibial (**minor**) and fibular (**major**) trochanters and may have one or (rarely) two more. The distal end of humerus and femur (**trochlea**) is adapted for hinge motion and is divided into inner and outer **condyles** for articulation with the zeugopodial bones, the proximal parts of the condyles being the **epicondyles.** Many reptiles and mammals have foramina near the lower end of the humerus (fig. 304), an **ulnar (entepicondylar) foramen** for the median (ulnar) nerve, and a similar **radial (ectepicondylar) foramen** for the radial nerve and brachial artery. Both foramina may coexist, usually but one is present, the ulnar in many mammals. Neither of these foramina is known in recent Amphibia or birds.

The radius serves as the axis around which the forearm revolves when the distal part of the arm is rotated, whence its name. The ulna often extends proximally beyond the articulation with the humerus, the projection being the **olecranon** on which the extensor muscles are inserted. Tibia and fibula resemble the bones of the fore limb, except in less rotational power and in the absence of anything like an olecranon.

The autopodium is divided into a proximal **basipodium** (wrist or **carpus**, ankle or **tarsus**), a **metacarpus** (palm) or **metatarsus** (instep), these forming the **mesopodium,** the autopodium terminating with the **metapodium** or **acropodium,** which includes the fingers and toes (**digits**), each composed of a number of segments (**phalanges**). The typical basipodium consists of nine or ten bones arranged in three transverse rows. The proximal row includes three bones. The one in line with radius or tibia is the **radiale** or **tibiale,** with **ulnare** or **fibulare** in a like position with regard to ulna or fibula. Between these two in either limb is an **intermedium.**[1] The distal basipodial row consists, typically, of five bones— **carpalia** in the hand, **tarsalia** in the foot—numbered from one to five, beginning at radial or tibial side. Between the proximal and distal rows of both hand or foot are one or two (rarely three) **centralia.** When three are present (embryo *Sphenodon* and some Theromorphs) one is exposed on the radial or tibial side.

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[1] It is uncertain whether the intermedium belongs to zeugopodium or basipodium It arises between the zeugopodial cartilages and later takes a basipodial position.

In man some of the typical (and primitive) bones of the basipodium have fused, and names are employed for all which differ from those of comparative anatomy, although sometimes used for lower groups, confusion resulting. Some of these names are common in older works and are given here, the less preferable in parentheses.

In the hand the **navicular (scaphoid)** is formed of radiale and usually a centrale, the latter sometimes remaining separate. The **lunatum (semilunar)** is the intermedium, the **triquetrum (pyramidalis)** the ulnare. Carpalia 1 and 2 are respectively **multangulum majus (trapezium)** and **multangulum minus (trapezoid)**; carpale 3 is the **capitatum** while carpalia 4 and 5 fuse as the **hamatum (uncinatum)**. In the foot tibiale and intermedium form the **talus (astragalus)** and when the centrale unites with the talus, the compound bone is the **tritibiale.** The fibulare is the **calcaneum (os calcis).** The first three tarsalia are the first, second and third **cuneiformia,** tarsalia 4 and 5 fusing as the **cuboid bone.**

The typical number of metacarpals and metatarsals is five, these being distinguished by number as are the digits. The thumb has the special name of **pollex,** the great toe is the **hallux.** None of the other digits of the foot have special names, the second of the hand is the **index,** the fourth the **annulus** and the fifth the **minimus.**

All of these bones of the appendages are preformed in cartilage. There may be others, some cartilage, some (**sesamoid**) ossifying directly in tendons or other connective tissue. ˙ Some of the additional cartilage bones are often interpreted as indications of additional digits—a **prepollex** or a **prehallux** (fig. 303), on the inner side of the hand or foot, a **postminimus** on the outer, most common in Amphibia and mammals. The hind limb often has an ossification, the **patella** (knee cap) in the extensor tendon which passes over the knee; a similar **brachial patella** is rare in the elbow. The **pisiforme** is a small bone on the ulnar side of the carpus of many mammals and some reptiles. It is said by some to have a membranous origin, by others that it arises in cartilage and is the remnant of a postminimal digit.

In the simpler Tetrapoda (Stegocephals, Urodeles) the limbs extend at right angles to the body axis, are bent downwards at elbow and knee, and at ankle and wrist they become horizontal, the digits pointing forwards and laterally. In higher Tetrapoda the stylopodia are normally parallel to the body axis, the humerus pointing backwards, the femur forwards. Without other modifications this would result in the digits of the hand pointing backwards; but there has been a torsion of the limb involving, first, the brachium (clearly

shown by the course of the nerve in figure 301) and another twist in the antebrachium, radius and ulna crossing each other when the hand is prone (fig. 315), so that, as may be seen in man or other plantigrade, the digits point forwards. The condyles of the lower end of the humerus are also involved in the twisting.

The chief movement of the paired fins of fishes is a fanning of the water, and largely in a single plane. In Tetrapoda other and different kinds of motion are called for, resulting in a change in the articulation of appendage and girdle. Instead of a simple hinge, there is usually a ball and socket joint, permitting motion in almost every plane. There has also developed capacity for more or less rotation of the distal
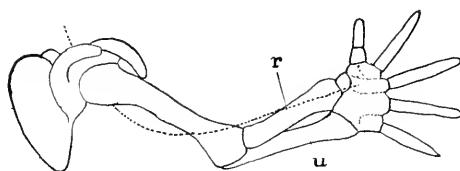
FIG. 301.—Torsion in developing human arm (Braus), *r*, radius; *u*, ulna. Dotted line, course of radial nerve.

parts, provided for by the two zeugopodial bones. The numerous joints of the autopodium accommodate the foot to unevenness of the ground and adapt it for numerous other purposes.

The difference in the uses of fore and hind limbs accompany changes in their relative size. In walking, the hind limb is flexed and thrust forwards, the foot placed on the ground, after which straightening of the limb *pushes* the body forwards. On the other hand the fore limb is straightened, extended forwards, and when the foot is on the support, flexure of the limb *pulls* the body along. Thus the hind leg is the more effective organ of terrestrial locomotion and this has resulted in its greater size, except in those forms (Ichthyosaurs, whales, etc.) which have reverted to the water or which (Pterodactyls, birds, bats) have taken to flight.

The feet are applied to the ground in different ways. The most primitive is where the metacarpals or metatarsals and digits rest on the surface (**plantigrade**). In **digitigrades** the mesopodial bones are lifted, and in **unguligrades** the weight is supported on the tips of the digits. Intermediate conditions between these three occur.

The skeletal parts of the appendages may be reduced in other ways than by fusion. In these reductions the more distal parts are first to disappear, the process proceeding proximally, digits being affected before mesopodial or basipodial parts. It is impossible to say there is any universal law in order of reduction other than this,

but at least in many cases the radial or tibial side of the appendage is first to show reduction, the fifth digit following.

AMPHIBIA.—The most primitive known Tetrapod limbs are those of Stegocephala; those of Urodeles, where the limbs still extend at right angles, are scarcely less primitive, the modifications being largely loss of parts. The posterior appendages of Anura have undergone the greatest modifications in connexion with their leaping habits. *Siren* (a Urodele) has lost the hind legs; while Gymnophiona and Aistopod Stegocephals have lost both pairs. All recent Amphibia have, at most, but four digits in the manus, unless parts in the Anura (p. 280) be remnants of pollex and prepollex.

STEGOCEPHALA have stout limbs, the humerus rarely with an ulnar (entepicondylar) foramen. Ulna and radius, tibia and fibula are never fused. The carpal elements are often unossified, but some species have two and even three centralia in the carpus. Most species have four digits in the manus, a few have five. The hind limbs are always pentadactyle, the second or third digit being the longest.

URODELA (fig. 302, *A*, *B*, *D*) have a relatively long humerus, ossified, usually, only in the shaft. It has radial and ulnar tuberosities for retractor and protractor muscles. Ulna and radius are separate, about equal, can be slightly rotated, and the ulna has an olecranon. The carpus is slightly ossified in Perennibranchs and some

FIG. 302.—*A*, carpus of *Cryptobranchus*; *B*, of *Triton* larva (Gegenbaur, '64); *C*, *Geotriton* (Baur, in Cope, '89); *D*, fore leg of *Diemyctylus*. *c*, centrale; *F*, fibula; *f*, fibulare; *H*, humerus; *i*, intermedium; *m*, metacarpals; *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare; 1–5, carpalia or tarsalia.

other genera. In the more typical species there are seven or eight slightly ossified carpal bones, including one (or two, proximal and distal) centralia and four carpalia. When, as in *Proteus* and *Amphiuma*, the digits are reduced to three, fusion of radiale and carpale 2, intermedium with carpalia 3 and 4, reduces the number of separate elements to three. It is not settled which digit is lost, probably 1 in all genera. No recent Urodeles have lost both pairs of legs, but apparently this was the case in the extinct *Lysorophus*.

The femur, only its shaft ossified, is long and has both tibial and fibular trochanters, one on either side of the head. Tibia and fibula are subequal in length and are separate. The foot, with few exceptions (*Proteus* down to two) has five digits and the tarsal parts are typical, except that two or three of the tarsalia may fuse, while occasionally there are two or three centralia.

ANURA have the humerus straight in many genera, but curved in many toads. It is longer than the forearm and usually has a single tuberosity. Ulna and radius are fused, but retain two articular surfaces at the distal end. Rarely (*Rana, Pipa*) a branchial patella occurs. The carpus is ossified, but the homologies of the seven ossicles of the adult are not certain, although the ontogeny is partly known. Besides the normal elements, one or two small bones may occur on the radial side often regarded as pollex and prepollex.

The saltatory functions of the hind limbs are correlated with structure, especially with the elongation of femoral, crural and tarsal regions. The femoral trochanters are weak or obsolete. Tibia and fibula are united, the line between them being most evident in *Pipa*, least so in *Rana*. No intermedium appears in ontogeny, there being two long bones—tibiale (talus, astragalus) and fibulare (calcaneum) in the proximal tarsal row. These are separate in *Bufo* and *Bombinator*, fused at both ends in *Rana* (fig. 303), throughout in *Alytes*. The tarsalia are reduced to from one to three small bones at the base of the first three metatarsals. No centrale is known, a fourth tarsale is said to fuse with the fibulare. The elements on the tibial side are often interpreted as prehallux (fig. 303).

FIG. 303.—Tarsus of *Rana*. *c*, centrale; *f*, fibulare; *m*, metatarsals; *ph*, prehallux; *t*, tibiale; 1–3, tarsalia.

REPTILIA.—Most reptiles have the body lifted slightly above the ground, the marked exceptions being the aquatic Ichthyosaurs, Sauropterygians, Thalattosaurs, some Chelonians and Pythonomorphs; and the flying Pterosaurs. Many Dinosaurs had bipedal locomotion. An aquatic life tends to shorten the stylopodial and zeugopodial bones, transforming the legs into paddles, this being accompanied by an elongation of the digits, either by lengthening the
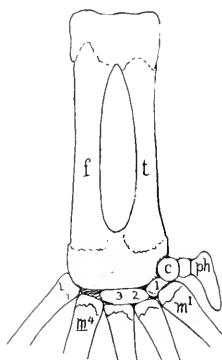
phalanges, as in marine Chelonia (fig. 308) or by increase in their number (Ichthyosaurs, Plesiosaurs, Pythonomorphs).

The humerus varies in shape and often has the ent- and sometimes the ectepicondylar foramen (fig. 304); it is usually shorter than the forearm. The ulna (often with an olecranon) is usually longer than the radius, these two bones being separate, the arm having slight rotatory powers. The femur has one or two trochanters, the fibular being most often lacking. Tibia and fibula are separate, the tibia the stronger of the two; its proximal end expanded and occupying most of the articular surface of the femur, the fibula articulating only with the posterior side of the thigh bone.
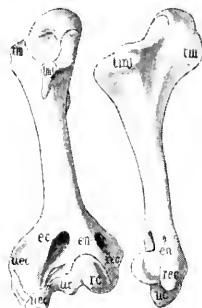
FIG. 304.   FIG. 305.

FIG. 304.—Left humerus of *Sphenodon* (Fürbringer, '00). *ec*, *en*, ect- and entepicondylar foramina; *tm*, *tmj*, tuberculum minus and majus; *rc*, radial epicondyle; *uc*, *uec*, ulnar condyle and epicondyle.

FIG. 305.—*A*, forefoot; *B*, tarsus of *Alligator* (Gegenbaur, '64). *AA*, intratarsal joint; *c*, carpalia; *F*, fibula; *f*, fibulare (calcaneus); *ic*, intracarpal joint; *m*, metacarpals; *R*, radius; *r*, radiale; *T*, tibia; *t*, tibiale; *tt*, tritibiale (astragalus); *U*, ulna; *u*, ulnare; 2–5, tarsalia; I–V, metatarsals.

The basipodia differ greatly in the various orders, but have the joint of the wrist and especially that of the ankle intracarpal or intratarsal (fig. 305), carpalia and tarsalia lying distal to the hinge. In most existing species tibiale and intermedium form a talus (astragalus) and a pisiforme is often present (this having been interpreted as a postminimal digit) and in Ichthyosaurs there are often two or more ossicles in line with it. Typically there are five digits, reduced to three in some Dinosaurs, the three toed feet having led to interpretation of the tracks on the triassic rocks of the Connecticut valley
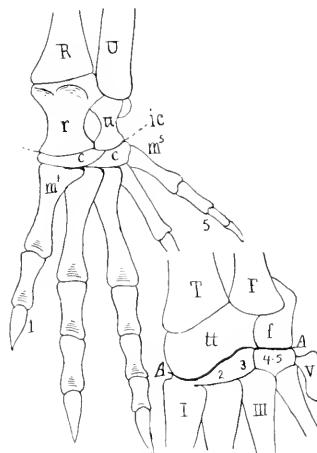
as having been made by birds. The reduction of the appendages reaches its extreme in apodal lizards and snakes, in which most, or even all traces of limbs are lost.

The ancestral reptiles undoubtedly were terrestrial, but some (some Chelonia, Ichthyosaurs, Pythonomorphs, Sauropterygia and Thalattosauria) returned to the water, while the Pterosauria took to the air. With these changes in habitat the limbs of the aquatic forms became paddles, the fore limbs of the Pterosaurs were transformed into wings. As in other cases of modification the stages of these changes may be reconstructed in the aquatic groups.

A webbing of the digits, as in marine turtles, prevents independent motion of parts; then increase in length and breadth of the limb made it a more effective paddle, increase in length being either by elongation of the phalanges (Chelonia), or by increase in their number (fig. 306) there being as many as twenty phalanges in some digits of Ichthyosaurs and Sauropterygians; and in some the paddle was widened by increase in the number of digits, either by division or by additions on either side. The efficiency of the muscles was increased by reduction of the proximal bones, the extreme being reached on some Ichthyosaurs where stylopodial and zeugopodial bones are polygonal and scarcely longer than the phalanges. The modification of the fore limbs of Pterodactyls for flight consist in the elongation of the bones of the forearm and the fifth digit to support the membranous, bat-like wing, the other digits, except the vestigial first, being more normal.

THEROMORPHA.—The limbs are less known than are the skulls. Most members of the group had an entepicondylar foramen (large in Therapsids) and some had one on the radial side. Therapsids also have a marked major tuberosity. The long ulna of Cotylosaurs has an olecranon. The hind limbs are much like the anterior, pentadactyly prevailing. Some had a single centrale, some more, and often all five tarsalia are distinct.

SAUROPTERYGIA have limbs which are not quite complete paddles, and fore limbs sometimes larger than the hind. The humerus is long and slender in the more primitive genera; in others it is short and stout, a radial epicondylar foramen occasionally occurring. Usually there are two proximal and five distal ossicles in the carpus, with a pisiforme and traces of a postminimus. Five metacarpals are present and the more primitive genera had the phalanges, numbering 2, 3, 4, 4, 3, in the digits, beginning with digit one, the number being increased to nine in some digits of later species. The pelvic limbs resemble the anterior pair except in greater reduction of the tarsal bones.

Ichthyosauria alsos how a progressive modification of the appendages, the earlier species having more normal limbs, the later being more paddle-like (fig. 306). In the latter radius and ulna are short and stout, the humerus having concave facets for articulating with the antebrachial bones. The carpus is incompletely ossified, the bones having an outer coat of cartilage. The pisiforme has two or three bones in line with it. A few species had but three digits, but in many there is a duplication of digits already referred to (p. 282). The femur is relatively longer than the humerus and has similar articular facets. In other respects the two limbs are much alike, the hinder being the smaller.
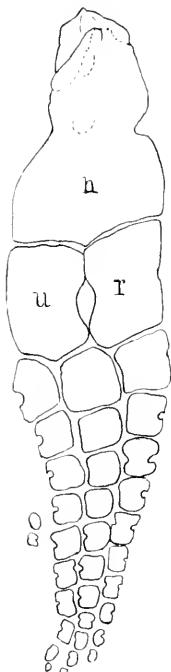
FIG. 306.—Fore limb of *Leptocheirus* (Merriam, '03). *h*, humerus; *r*, radius; *u*, ulna.
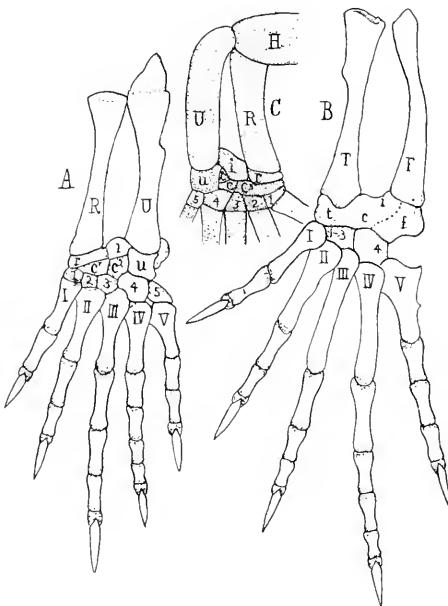
FIG. 307.—*A*, fore limb and *B*, hind limb of *Sphenodon* (Osborn, '03); *C*, carpus of developing *Sphenodon* (Schauinsland, '03). *c*, centralia; *F*, fibula; *f*, fibulare; *H*, humerus; *i*, intermedium; *R*, radius; *r*, radiale; *T*, tibia; *t*, tibiale; *U*, ulna; *u*, ulnare; I–V, metacarpals or metatarsals; 1–5, carpalia or tarsalia.

RHYNCHOCEPHALIA.—In *Sphenodon* and the more typical fossil genera the short humerus (fig. 304), expanded at both ends, has both epicondylar foramina, but some fossils have only that on the ulnar side. Usually the carpus is primitive and *Sphenodon* (fig. 307) has radiale, intermedium and ulnare, and in the embryo three centralia

(fig. 307, C), reduced in the adult to two. The five carpalia are separate. Both trochanters are close to the head of the femur. The tarsus is reduced, one of the centralia taking part in forming a tritibiale, and only three tarsalia are present. The most aberrant fossils, the Thalattosauria, have the proximal appendicular bones short and stout, in accord with the aquatic life. The distal elements are unknown.

SQUAMATA.—A few lizards are limbless, some have the limbs greatly reduced. In normal genera the humerus has a roller head between two well-developed tuberosities, and the dicondylic lower end has an entepicondylar foramen. The ulna, stronger than the radius, usually has an olecranon, and in many genera the lower end of the radius is expanded. The carpal hinge is markedly intracarpal. The intermedium, distinct in the embryo, fuses with the centrale (some have two centralia), the compound bone lying between radiale and ulnare. The five carpalia are usually separate and the corresponding phalanges are 2, 3, 4, 5, 3, but occasionally the fifth digit has four or five phalanges. The digits of Chameleons are grouped in two bundles, 1 and 5 being opposed to the others. The digits are reduced to three in *Seps*, *Chalcides*, etc., and reduction reaches its extreme, short of entire loss, in some skinks.

The femur is usually longer than the humerus and has only the fibular trochanter, and the head is little prominent. Most species have a patella. In the tarsus the fibulare enters a tritibiale, the resulting 'astragalus' articulating with both crural bones, the intratarsal hinge being distal to it. The tarsalia are reduced in number by fusion, so that in some genera only 3 and 4 are distinct. The foot is usually pentadactyle with a phalangeal formula 2, 3, 4, 5, 4. In *Pseudopus*, *Pygopus*, etc., the foot is simple, there being no division into digits, and in *Ophisaurus*, *Aniella*, *Acontias*, *Anguis*, etc., all limbs are lacking.

PYTHOMOMORPH appendages have many of the characters of other marine reptiles (p. 282), the bones of the upper arm being short and broad, the radius with its lower end expanded. The carpals vary from seven in *Clidastes* to two in *Mosasaurus* and *Tylosaurus*. There were five digits with few phalanges in *Clidastes* and *Mosasaurus*, but increased to eleven or twelve in *Tylosaurus*. The hind limb, except in smaller size, is much like the other. The tarsal bones are from one to three, and the four or five digits have a varying number of phalanges.

OPHIDIA, with few exceptions, have lost all traces of paired append-ages, but a few have retained the pelvis (p. 265) and some bones of the hind limbs, (fig. 286, *D*), interpreted as femur and tibia.

CHELONIA have a short, usually curved humerus, the head of which is sometimes hemispherical, sometimes a roller, while distally there is usually an entepicondylar foramen, and the trochlea is divided into three condyles, and many species have a brachial patella (p. 277). The ulna, smaller than the radius, has an olecranon, and both of these bones are immovable on each other in some species. The carpus is primitive in most genera, inter-medium and centrale (sometimes two centralia) being separate, but the radial centrale, when there are two, may fuse with the radiale. A pisiforme of varying size occurs. On the distal side of the carpal hinge the five carpalia are usually separate, each supporting its metacarpal. The digits are short in terrestrial and fresh-water gen-era, elongate in marine. The phalanges are usually 2, 3, 3, 3 or 4, 2 or 3, rarely 2.2, 2, 2, 2.

The femur, often curved, but straight in marine genera, has a hemispherical head at nearly a right angle with the shaft, and near it is a large fibular trochanter. There are two distinct condyles at the lower end, and sometimes a

FIG. 308.—*A*, Fore limb of *Chelone imbricata*, and *B*, hind limb of *C. midas* (Reynolds, '97). *c*, centrale; *F*, fibula; *f*, fibulare; *Fe*, femur; *h*, humerus; *i*, in-termedium; *m*, metacarpals and meta-tarsals; *p*, pisiforme; *R*, radius, largely hidden by ulna; *r*, radiale; *T*, tibia; *tt*, tritibiale; *U*, ulna; *u*, ulnare; 1–5, carpalia and tarsalia.

patella. The tarsus is primitive in some, all nine bones being present, but usually there is a fusion of tibiale, intermedium and centrale (sometimes two centralia) to a tritibiale (astragalus), the intratarsal hinge passing between this on the one side and fibulare and tarsalia on the other. Fusion is common between tarsalia 4 and 5, while the fifth sometimes unites with the fourth or fifth metatarsal.

CROCODILIA.—The stout and slightly curved humerus is expanded at both ends and has a strong radial (deltoid) crest. The trochlea

is divided into two condyles, with an entepicondylar groove or foramen above. Radius and ulna are nearly equal, the olecranon moderate or obsolete. The carpus (fig. 305) has been greatly modified in recent species where it has two proximal and two distal bones. The proximal (the intermedium probably fused with one of them) are the larger, while in the distal row the bone on the radial side is the fused carpale 1 and the two centralia; the second carpale has united with the second metacarpal, while carpalia 3 to 5 have united as the ulnar element, near which is a large pisiforme. The phalanges are 2, 3, 4, 4, 3.

The round head of the femur scarcely projects from the shaft, the weak fibular trochanter is a long ridge, the tibial trochanter is reduced and the distal end of the femur has two articular surfaces. The tibia, larger than the femur, occupies most of the articular surface of the femur, and distally it articulates with the tritibiale, the fibula touching both this and the fibulare. Tritibiale and fibulare are larger than the other tarsal bones, one of which is formed of tarsalia 1 to 3, the other of 4 and 5. The intratarsal hinge is like that of Chelonia. The fifth digit is rudimentary, and consists of a short metatarsal attached to the fibular tarsale.

FIG. 309.—*A*, hind foot of *Antrodemus valens* (Gilmore, '20); *B*, fore foot of *Allosaurus fragilis* (Gilmore, '15). *a*, talus; *c*, calcaneum; *f*, fibula; *h*, humerus; *j*, intratarsal joint; *m*, metatarsals; *r*, radius; *re*, radiale; *t*, tibia; *u*, ulna; 1–3, digits (Gilmore's numbering).

DINOSAURIA.—The limbs of Dinosaurs are less known than most of the axial skeleton, least known in the distal parts. Sauropods and some Ornithischia had solid bones, others had them hollow and possibly pneumatic. Fore and hind limbs are nearly equal in Sauropods; in Theropods and many Ornithischia the fore limbs are much smaller than the hind, indicating a bipedal locomotion. The Sauropods are plantigrade, with hoofed digits, the other sub-orders digitigrade (fig. 292), some having prehensile claws. The basipodal parts were incompletely ossified, the distal row being rarely represented in the fossils.

The humerus usually has a strong crest for the radial tuberosity. Both radius and ulna are well developed, the latter with a strong olecranon. The functional digits vary from five to three, the others showing various degrees of reduction. The strong femur (enormous in some species) has a middle trochanter except in the armored Stegosaurs. Tibia and fibula are complete and the

former has a strong cnemial crest (fig. 310, c). Tibiale and intermedium are fused (astragalus, talus) the pisiforme sometimes being included in this bone. Its intermediate part extends up on the lower end of the tibia, fusing with it in *Triceratops*. In some species the calcaneum projects like a heel. The tarsalia persist in part in some Stegosaurs. The digits vary between three and five, and the phalanges are very variable in number.

PTEROSAURIA.—The limb skeleton of the wings differs from that in other flying Vertebrates (birds and bats). The moderate humerus has an expanded deltoid crest. Radius and ulna, about equal, are sometimes twice the length of the humerus, and their ends are but little expanded. The carpal bones are in two rows, the proximal with two ossicles, while the three or four carpalia are sometimes fused. Apparently the first metacarpal is lost, the remaining four are subequal, (sometimes as long, sometimes half as long as the fore arm, but the fifth is much stronger than the others which may be reduced to mere threads. The fifth supports the greatly elongate fifth finger which is the main support of the bat-like wing. Metacarpals 2 to 4 bear the small digits of the corresponding fingers which are free from the wing. The femur has a weak trochanter. The tibia, as in birds, is longer than the femur, but the fibula is reduced, its pointed lower end reaching to about the middle of the tibia, with which it may fuse. There are two proximal tarsal bones, sometimes fused with the tibia. There are at least three tarsalia and five metatarsals, the fifth short and sometimes bearing no phalanges.

AVES.—Although very different in external appearance and in use, the wing and leg of a bird are much alike in structure, and what differences occur are largely confined to the distal parts which, in the wing, have been more modified than in the leg. Reduction has gone so far that in some fossils no trace of a wing has been found, while many moas lack a humerus.

FIG. 310.—Hind foot of *Megacerops tyleri* (Lull, '05). *Fe*, femur; *F*, fibula; *T*, tibia.

In all recent birds the humerus is long and slender (fig. 311), its proximal end expanded and having a rather long articular surface which fits in the glenoid fossa. Both radial and ulnar tuberosities (sometimes long crests) are present, the ulnar containing the opening to this highly pneumatic bone. The two distal articular surfaces are separated by a groove, most marked on the palmar surface. Paseres often have a brachial patella between humerus and fore arm.

The fore arm, except in *Archæopteryx*, is longer than the humerus, its bones are slender, the ulna stronger than the radius and usually showing tubercles on the lower side, caused by the bases of the feathers; it also has an olecranon and there may be a small accessory bone at the lower end of the radius over which the extensor tendon passes.

The acropodium, relatively longest in fast fliers, is most modified. The carpus has the same intracarpal joint, accompanied by reduction of the carpal elements, there being at most, in the adult, two of these (the homologies of which are uncertain), in recent and fossil
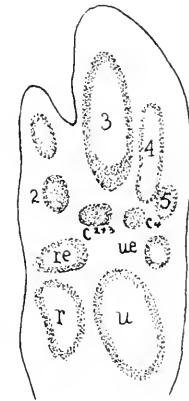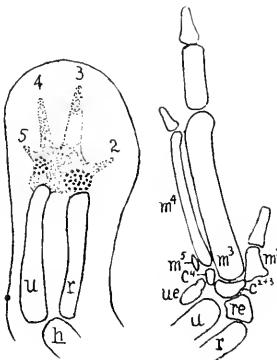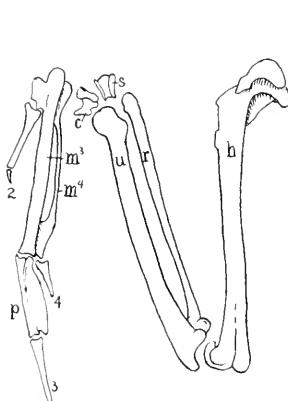
FIG. 311.—Wing of *Clangula* (Shufeldt, '09). *c*, cuneiforme; *h*, humerus; *m*, metacarpals; *p*, phalanges; *r*, radius; *u*, ulna; 2–4, digits.

FIG. 312.—*A*, *B*, Two stages in development of wing of *Sterna* (Leighton, '94); *C*, developing wing of *Cypselus* (Zehntner, '90). *c*, carpalia; *m*, metacarpals; *h*, humerus; *r*, radius; *re*, radiale; *u*, ulna; *ue*, ulnare; 2–5, digits.

birds. The upper and smaller of these articulates with the radius and most of the metacarpals and rests against the ulna. The other (lacking in *Apteryx*, *Casuarius* and *Dromæus*) lies in the angle between ulna and metacarpals which extend to the ulna. In the young there are at least two carpalia which fuse early with the metacarpals. In the metacarpus two bones are fused at their ends in modern birds (three separate metacarpals in *Archæopteryx*) usually with a gap between them. Another smaller bone projecting from the radial side of the first, is another metacarpal; it varies in length and bears one or two phalanges. Digit 3 is the longest and usually has two phalanges, the ulnar digit is much like radial.

There has been much discussion of the numbering of the avian digits—1, 2, 3; 2, 3, 4; and 3, 4, 5. Since several birds have an additional metacarpal in the

embryo on the ulnar side (fig. 312) of the last persisting digit, with which it soon fuses, it follows that the numbering 3, 4, 5 cannot hold. Analogy with other animals (p. 279) would tend to show that digit one often is the first to disappear, thus affording support to the numbers 2, 3, 4 adopted above.

Sometimes digit 3 has three phalanges, and then digit 2 has two. *Archæopteryx* (which possibly used its digits in part for grasping) has the phalanges 2, 3 and 4. Penguins lack digit 2, 4 being very long. Some Struthionines have only digits 3 and 3, *Apteryx* and *Dromæus* only 3.

As it is the only locomotor appendage in walking or swimming, the leg is usually strong and sometimes (wading birds) is very long. The femur is relatively short and stout; its head and neck are at right angles to the shaft, the hemispherical head having a groove for the teres ligament. The shaft is directed forwards so as to bring the centre of gravity over the feet. The upper end has both tibular and fibular trochanters, which, owing to the torsion of the bone, face backwards and forwards respectively. A patella is common. In the crus the tibia is strong, the fibula reduced and often fused with the tibia, its lower end never reaching the tarsus, its upper end always articulating with the femur. The tibia usually has one or two anterior (cnemial) ridges for origin of the foot muscles and its lower end has two pulley-like articular surfaces, separated by a groove (sometimes bridged by bone) for the passage of a tendon.

The tarsus is reptilian in its intratarsal joint. The embryo has three proximal tarsal cartilages which soon fuse as the 'astragalus;' this has an ascending process, the intermedium, extending up on the tibia. Soon the astragalus fuses with the tibia to a **tibiotarsus,** the astragalus remaining distinct only in *Apteryx*. From one to four tarsalia appear in the embryo and soon fuse with the proximal ends of the united meta-tarsals, the result being a **tarsometatarsus** (fig. 313), the tarsal bones thus being lost as separate bones in the adult.

FIG. 313.— Tarso - m e t a - tarsus of swan (Q u e n n e r - stedt, '72, in Bronn).

There are, at most, but two tarso-metatarsal bones in the adult. The larger of these varies in length, being very long in wading birds, shortest in penguins. Its ends are expanded, the upper having two articular faces, the lower three pulleys (fig. 313), an evidence of the compound nature of the bone. The other metatarsal, when present, is at some distance down on the tibial side and disappears with the

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corresponding digit. Most birds have four digits in the pes, the tibial one turned backwards, and in parrots (fig. 314) and many other climbing birds the last toe on the fibular side is also reversed. In some 'Palmipeds' all four toes are directed forwards. Cassowaries, *Rhea* and some woodpeckers have only three digits, the African ostrich (*Struthio*) but two, apparently 3 and 4. There is little evidence as to whether digit 1 or 5 is lost in most birds; the usual statement is that 1, 2, 3, and 4 persist.

Archæopteryx has a relatively strong femur, distinct tarsal bones and four toes. The fibula is free in moas, longest in penguins (which have short metatarsals) and some Raptores where it nearly reaches the tarsal joint. The 'Dorking fowl' are the only exception to the rule of four toes or less, these having five, the additional toe being thought to arise by the division of 1, but explicable also on the supposition that the first, not the fifth is lost in other birds. This fowl also has an increase in the number of phalanges.

Fig. 314.—Foot of parrot (*P. amazonicus*). *f*, femur; *fb*, fibula; *p*, patella; *tm*, tarsometatarsus; *tt*, tibio-tarsus; II–V, digits.

MAMMALIA. — The mammalian appendages, primitively adapted for walking and running, undergo, in the several orders greater modifications, especially in the fore limb, than in other classes of Vertebrates, becoming changed into organs for leaping, digging, grasping and climbing, swimming or flying; uses paralleled to some extent in Sauropsida. Yet, in all mammals, the Tetrapod structure is retained. The more primitive groups are plantigrade, this feature being retained even in Primates. Others are digitigrade, and lastly Ungulates and Proboscidia are unguligrade.

In limb structure the lower mammals are primitive, and much like the Stegocephals and the less differentiated Theromorphs; in the more specialized mammals several modifications appear. The fore limb has become strongly reversed, the elbow pointing backwards, resulting in a twisting of the humerus so that the dorsal side of the

Amphibian limb now faces the rear, the hinge being transverse to the axis of the body. To bring the digits of the manus so that they point forwards, the fore arm has a twist in the opposite direction, the radius crossing the ulna so that digit 1 is on the medial side of the appendage (fig. 301). Some (*e.g.* Ungulates) move the limb like a pendulum in a single plane; in others (the extreme occurring in man) it may be swung in almost every plane, this freedom of motion at the shoulder being correlated with greater capacity of rotation of ulna around the radius, so that in man the hand can be turned through 180°, either palmar or dorsal side being downwards. There is less torsion of the hind limb, but, on the other hand, there is more modification, chiefly by fusion, here.

FIG. 315.—Diagram of torsion of fore-arm bones (Bütschli, '10). *A* is the primitive condition with the elbow pointing outwards; *B* with the elbow directed backwards as in Mammals, the limb parallel with the side of the body.

The humerus, short in Ungulates, boscidia and swimming mammals, is usually as long as the fore arm, rather slender and slightly curved. The head is somewhat roller-like in the primitive orders, and the limb

FIG. 316.— Humerus of *Dasypus;* the arrow passes through the entepicondylar foramen.

moves in a plane parallel with the axis of the body; elsewhere it is hemispherical, giving the limb greater freedom of motion. Both tuberosities are well developed, especially in digging genera (moles, anteaters, etc.), accompanied by a shortening of the whole limb. The tuberosities are long crests in some Primates and bats. The distal end of the humerus has one or two rollers for the ulna (when two, separated by a groove), and a hemispherical capitular head for the head of the radius. The epicondyles are connected with inner and outer articular surfaces, and on the posterior side is a pit or groove (often perforate) between the condyles, to receive the olecranon. An entepicondylar foramen is common (fig. 316) though lacking in Cetacea, recent Ungulates, most rodents and bats, and some other forms including man.

The fore arm is long in bats and a few rodents. Both ulna and radius are present and usually well developed. The most important articulation with the humerus is that of the ulna, which has a sigmoid groove for the trochlea, and proximal to this is the olecranon, (rudimentary in Ungulates) which makes the ulna longer than the radius. Both bones articulate, as a rule, with the carpus, but where much rotation is possible, the radius is expanded distally, giving a larger surface for articulation with the carpus, and it may have a **styloid process** on its outer border.

The ulna is reduced in several mammals belonging to different orders. Thus in bats it is slender, and here, as in horses, camels and some Ruminants it may fuse with the radius, its proximal part being lost in the horse, its distal part fusing with the radius in bats, and little more than the olecranon remaining in Ruminants.

The number of carpal bones ranges from ten or eleven in the embryo to as few as five, arranged in two rows, in some adults. This reduction is due, in part, to the absence of one or more cartilages in the embryo, more to the fusion of elements, and still more to loss accompanying the loss of digits. Radiale, intermedium and ulnare usually retain their individuality and are the larger carpal bones, but radiale and intermedium often unite as a **scapho-lunatum.** Some embryos have two centralia, but usually only the radial of these is present, while in some species no centrale is known. The ulnar centrale may fuse with intermedium or with carpale 2 or 3; the radial centrale commonly unites with the radiale. Except in whales, carpalia 4 and 5 unite as a hamatum. The fusions and reductions of the carpal bones is greatest in Ungulates.

The metacarpals are usually long and slender and undergo reductions closely related to those of the digits. These latter vary from the normal five, to one. Typically the phalangeal formula is 2, 3, 3, 3, 3, and only rarely, when all digits are present, fingers 2, 3 and 4 may have two phalanges each. The terminal phalanx is often split or grooved on the dorsal side for the support of a claw.

Besides these normal parts other bones may develop on both radial and ulnar sides—prepollex and postminimus (p. 277), the most common being the pisiforme on the ulnar side which in several rodents, may have two joints. The prepollex is less common, except in digging or swimming species with broad hands. It is two jointed in a few species.

As in Plesiosaurs and Ichthyosaurs the number of digital bones may be increased in whales, not by multiplication of phalanges, but by the retention of separate epiphyses through life.

The femur, relatively short in Monotremes, Ungulates, seals and whales, usually has a hemispherical head on a short neck which extends at an angle with the shaft, but in Monotremes and some Ungulates and Edentates it is in line with the axis of the bone. Major and minor trochanters are variously developed, and a third trochanter, common in Perissodactyls, Insectivores, some Edentates, rodents, etc., may be connected with the major trochanter by a long (gluteal) crest. Distally the femur has two condyles, lateral and medial, for articulation with the crural bones, the tibial connecting with both, the fibula, when not fused with the tibia, articulating with the lateral condyle. There is usually a patella at the knee (small in Carnivores, possibly lacking in some Marsupials) and there may be similar bones (**fabellæ**) in the genal angle.

The tibia is always the larger of the two crural bones, the fibula is often greatly reduced. These two bones are parallel, no twisting occurring, and they have but slight motion on each other, the extreme occurring in some Marsupials with opposable great toe, when there may be slight rotation. Partial fusion of the two, especially at the ends, is common. The tibia has two articular surfaces for the two femoral condyles; distally it articulates with the talus, and medial to the articulation it sends a process (**medial malleolus**) down on the medial side of the ankle. Usually the fibula does not reach the femur and its lower end often falls short of the tarsus. It is most reduced in bats where its distal end, fused with the tibia, forms a **lateral malleolus** (occurring also in other orders), the two malleoli strengthening the tarsal joint.

The tarsus is usually short *Tarsius* (fig. 324) and some lemurs excepted. There are two bones in the proximal row, a median talus (astragalus) and a lateral calcaneus. The former is usually fused tibiale and intermedium, the latter the fibulare, but in some species the talus may include the centrale (tritibiale), or the latter may fuse with the calcaneum. The intratarsal joint of the Sauropsida does not occur in mammals, the hinge being between the crural and proximal tarsal bones, talus and tibia being most concerned, fibula and calcaneus articulating only in Aplacentals and a few others. The

calcaneus often projects backwards for the insertion of the tendon of Achilles.

The other tarsal bones fuse in various ways, often accompanied by reduction of digits and metacarpals. The centrale, when distinct, is the scaphoid (navicular) of human anatomy, the tarsalia have specific names which were given on p. 277. The third digit is usually the longest, but Artiodactyls have 3 and 4 equal and 1 and 5 are largest in Pinnipeds where they support the margin of the flipper. The hallux is opposible to the other digits in Primates and a few members of other orders. In mammals with great leaping powers metatarsals 3 and 4, fuse to a long 'cannon bone,' and the same name is given to the third metatarsal of Perissodactyls. In the former group metatarsals 2 and 5 are reduced to 'splint bones;' in Perissodactyls metatarsals 2 and 4 have this name, all being short rudiments at the proximal end of the cannon bone, with which they may fuse.

Fig. 317.— Foot of *Talpa* (Flower, '85). *f*, falciform bone; *i*, intermedium; *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare; 1–5, digits.

MONOTREMES have an entepicondylar foramen in the humerus; radiale and intermedium form a scapholunatum, and all feet are plantigrade pentadactyle. The fibula does not form a malleolus, although it articulates with both talus and calcaneus.

MARSUPIALIA usually have the entepicondylar foramen; radius and ulna can be slightly rotated, radiale and intermedium are usually separate, the latter small. A separate centrale does not occur in the adult. The five digits of the manus are normal, except in *Perameles* where 4 is rudimentary, 1 and 5 are lost and the metacarpals are long. The femur lacks the third trochanter; tibia and fibula have slight motion on each other in arboreal species, but their distal ends are often fused in other species. The digits are variously modified; in kangaroos 1 is lost, 2 and 3 are reduced and 4 is longest and strongest.

INSECTIVORA.—The humerus has an entepicondylar foramen; this bone being peculiar in shape in Talpids. All five digits of the manus are usually present, the pollex never being opposible. *Chrysochloris* is noteworthy for having the phalangeal formula 2, 2. 1, 3, and for having only carpale 3 and the hamatum in the carpus. Other genera often have digit 3 elongate and a separate centrale. The fossorial species have the prepollex developed as a large **falciform bone** (fig. 317). A third trochanter on the femur is all but unknown; tibia and fibula are fused distally. The tarsus is sometimes elongate; digit 1 is lacking in some. *Chrysochloris* has two phalanges in each toe.
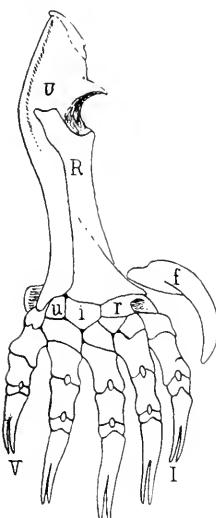
CHIROPTERA.—The humerus, which lacks the ulnar foramen, has strong tuberosities in most genera. The radius is longer than the humerus, sometimes as long as the body. Only the distal part of the ulna, which fuses with the radius, and the olecranon persist. The wrist (fig. 318) has two well-marked joints, one between radius and carpus, the other between carpus and metacarpus. The centrale and the three proximal carpal bones are usually fused. Carpale 1 supports the pollex, the only normal digit, the others being very long to support the wing. The pisiforme is in the middle of the carpus. The femur has no third trochanter, the fibula is degenerate, only its distal end, fused with the tibia, remaining. Talus and calcaneus are long, the latter with an osseous spur. The five toes are clawed.

DERMOPTERA, represented only by *Galeopithicus*, has a scapho-lunatum and no free centrale. Digit 5 of the manus is longest, followed by 4; 1 is much shorter than the others. The small fibula is complete, but does not reach the calcaneus. The five clawed toes are nearly equal.

EDENTATA have the humerus long and slender in sloths, in other genera (figs. 272, 316) it has strong tuber-osities and an entepicondylar foramen. Radius and ulna are separate and in Xenarthra have slight rotational powers. Radiale and interemdium are separate in Xenar-thra and Tubulidentata, fused in pangolins. The other carpal bones are usually distinct, except that a centrale only

FIG. 318.— Carpus of fetal *Rhinolophus* (Gegenbaur, '64). *c*, centrale; *i*, interme-dium; *u*, ulnare; 1–5, carpalia; I–V, meta-carpals.

occurs in *Tamandua*, while the distal carpals may be united, and in sloths, fused with the partly united metacarpals. The carpal bones may be increased by sesamoids. The number of digits in the manus ranges from five in Pholidota and some Xenarthra, to four in other Xenarthra and the aard vark, digits 3 and 2 usually the larger. The femur, short in sloths where it lacks strong trochanters, has a third in Tubulidentata and most Xenarthra. The crural bones are separate in sloths and anteaters; elsewhere tibia and fibula fuse, proximally or distally, or (*Dasypus*) at both ends. Fusion of the tarsal bones is common, and in sloths the tarsalia may unite with the metatarsals. Usually the foot is pentadactyle, digit 1 being absent occasionally and 5 in a few. The distal phalanges of all may be grooved or cleft for the claws.

RODENTIA commonly have an entepicondylar foramen in the humerus. Radius and ulna are always separate, but radiale and intermedium are united and there is a radial sesamoid, even when the pollex is reduced. Prepollex and postminimus are common, the former sometimes with a claw, the latter may have two phalanges. There may be a third trochanter on the femur; tibia and fibula are separate or fused distally, the fibula rarely articulating with the calcaneus. A prehallux is common, and both fore and hind feet almost always have five digits.

CARNIVORA have the limbs very different in the two suborders. In the Fissipedia they are adapted to terrestrial locomotion; in the Pinnipedia (seals, etc.) for aquatic life. The long humerus of the Fissipedia has an ulnar foramen in recent cats and some Mustelids; its tuberosities are large and there is a large deltoid process and a deep fossa for the olecranon. Ulna and radius are separate

and the olecranon is large, the distal end of the ulna being the smaller. In recent species there is a scapho-lunatum with which the centrale unites in the adult. Rudiments of the first digit are always present, (smallest in *Hyæna*) even when the first metacarpal is rudimentary, the digit itself is reduced in Felidæ and Canidæ. The femur has no third trochanter and the crural bones are separate. The articular surface of the talus is deeply excavate. Dogs (except some domesticated races) and cats have a vestigial hallux; the dachshund has a double great toe.

The Pinnipedia have short stylopodial and zeugopodial bones and no entepicondylar foramen, and the femur lacks a third trochanter. The carpus (fig. 319) and tarsus are much like those of Fissipeds. The hind feet are rotated backwards so that they are nearly parallel with the body axis, the outer digits of the feet being longer than the others.
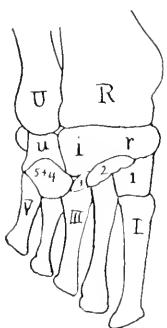
Fig. 319.—Carpus and metacarpus of walrus (Murie) *i–r*, scapho-lunatum; *R*, radius; *U*, ulna; *u*, ulnare; 1–5, carpalia; I–V, metacarpals.

CETACEA have practically lost the hind limbs· the anterior are modified into swimming flippers, short in Mystacocetes, long in Denticetes, especially long in *Megaptera*. With this there is a great reduction in the length of the separate bones. The entepicondylar foramen is lost, radius and ulna are parallel and similar, sometimes partly united. The carpus in pentadactyle Denticetes is much like that of normal mammals and may have two centralia. Some have five separate carpalia, but usually there is fusion and loss, so that dolphins with four digits have three carpalia (some say these are 2, 3, 4, others that 3 is lost, 1 persisting). There are four or five digits, the phalanges having little motion on each other, though joints remain at elbow and wrist. An increase in the number of phalanges is common, the extreme reached in *Globiocephalus* where the formula is 4, 14, 11, 3.1. This may be the result of actual increase of phalanges or the persistence of epiphyses as separate bones.

UNGULATA, in foot structure, present two different lines. If fossils be considered, the order must be enlarged to include groups (Hyracoids, Proboscidians and several extinct associations) usually regarded as orders. The fossil groups are scarcely considered here, nor is there an attempt to decide whether modern Ungulates are diphyletic as has been argued. The characters of limb structure of an ancestral group have been summarised by Weber as follows:

"Humerus with entepicondylar foramen, strong tuberosities and shallow condyles; radius and ulna separate, carpus with centrale; trapezoid and capitatum (carpalia 2 and 3) small. Femur with third trochanter; tibia and fibula distinct, latter articulating with talus, scarcely or not with calcaneus. Talus with neck and articular head for the naviculare (centrale), its surface for the tibia restricted, behind with an opening (foramen tali). A tibiale tarsi above the ectocuneiforme (tarsale 3). Pentadactyle; ungual phalanges in the older members little broadened, Plantigrade or at most semiplantigrade."

There are two types of basipodal structure in Ungulates (sens. lat.). The **taxeopodous** group has proximal and distal tarsal bones in straight lines parallel

with the axis of the limb, a condition largely retained in Hyracoids and Probos-cidians (fig. 323). **Diplarthrous** tarsi have a strong tendency towards alterna-tion of the elements of the two rows so that each proximal bone articulates with two of the distals, as in all recent true Ungulates.

The common features of all are a short stout humerus with large external tuberosities and no ulnar foramen; ulna and fibula incomplete; carpus and tarsus diplarthrous, the talus articulating with central (navicular) and calcaneus, the centrale with carpalia 2 and 3. The femur has the head separated from the shaft by a neck. The pollex is greatly reduced or absent; a well-developed patella is present. The recent species fall into two lines, Perissodactyla and Artiodactyla (fig. 320). In the first the femur has a third trochanter and the

axis of the limb passes through digit 3, around which the other digits are symmetrically arranged. Artio-dactyls lack the third trochanter and have the pedal axis running between digits 3 and 4, which are about equal. From the prominence of digit 3 in Perisso-dactyls, of 3 and 4 in the other group, these toes support most of the body weight, the lateral ones tending to degenerate, the extreme of this being in modern horses where only 3 persists, except as repre-sented by the greatly reduced metacarpals and meta-tarsals; and in Tylopoda where only digits 3 and 4 are retained.

The extinct orders of Ungulates are largely based on foot structure, and usually have taxeopodous feet, these occurring in all feet of Ancylopoda, Condylarthra, Litopterna and Amblypoda and at least in the tarsus of Toxodontia and the carpus of Typotheriidæ, the latter family having the ente-picondylar foramen. A few have the third trochanter.

In PERISSODACTYLA (fig. 321) the head of the humerus projects slightly, the tuberosities are short and strong, and its distal end is transversely truncate. Ulna and radius vary with the foot structure; the radius, large at both ends, is constant; the ulna being well developed and separate in tapirs and *Rhinoceros; Mac-rauchenia* has the two bones fused and in horses the ulna persists in the ole-cranon and a tapering part fused with the radius. The third digit is always the strongest, and with its preeminence the carpal bones are modified in correlation with the reduction of the digits, but radiale and intermedium do not unite. The modifications are most marked in the lateral bones. *Hippopotamus* has digits 2 and 4 nearly as large as 3, and *Tapirus* has 5 large, but not functional. Other genera show a progressive reduction of the lateral digits (evident in the history of the horse) until in modern *Equus* the third digit alone is functional and all that remains of the lateral digits are the pair of splint bones at the upper end of the
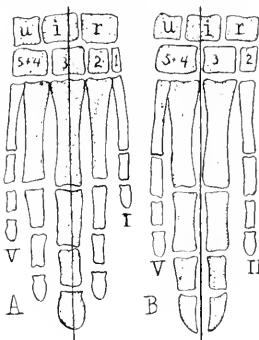
Fig. 320.—Schema of bones in manus of (A) a Perissodactyl (horse) and (B) Artiodactyl (cow), (Weber, '04). The shaded parts are those retained from the primitive five dig-its; the straight line is the axis of the appendage. *i,* intermedium; *r,* radiale; *u,* ulnare, 1–5, carpalia; I–V, digits.

third metacarpal. Usually the distal phalanx of each persisting digit is broadened to support the hoof.

The femur, longer than the tibia in tapirs, always has the third trochanter, and a nutrient canal enters the bone at about the middle of the posterior side. Rhinocerotidæ and Tapiridæ have separate crural bones, but in horses the fibula remains only proximally, fused with the upper end of the tibia. The tarsal
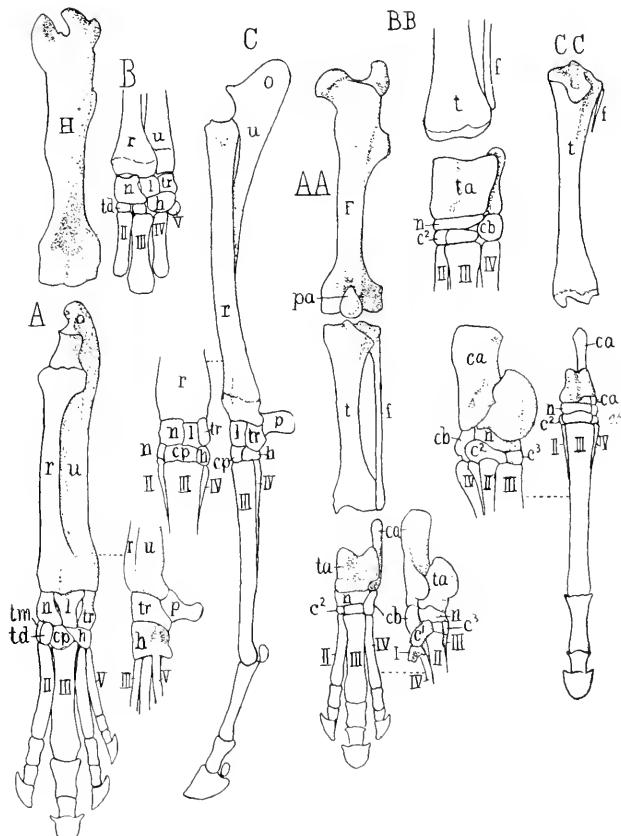
FIG. 321.—Feet of Perissodactyls: A, AA, fore and hind feet of *Tapirus*; B, BB, of *Rhinoceros*; C, CC, of *Equus* (Bütschli, '10). c^{1-3}, cuneiformia; *ca*, calcaneum; *cb*, cuboid; *cp*, capitatum; *F*, femur; *f*, fibula; *H*, humerus; *h*, hamatum; *l*, lunatum; *n*, naviculare; *o*, olecranon; *p*, pisiforme; *r*, radius; *t*, tibia; *ta*, talus; *td*, trapezoid; *tm*, trapezium; *tr*, triquetrum; *u*, ulna; I–V, metacarpals and metatarsals.

bones are in two rows, the talus with two unequal articular faces. The feet are never plantigrade, the third toe always the largest. Tapirs and *Aceratherium* have five toes arranged symmetrically about 3; others have the lateral digits more elevated, 1 being often lost, followed in modern horses by 2 and 4, traces of them being the splint bones fused with the cannon bone.

The ARTIODACTYLE feet (fig. 322) are characteristic in the fusion of meta-carpals and metatarsals 3 and 4 to a cannon bone which shows its double origin, especially at the distal end, in Suina and *Hippopotamus*. Metacarpals 2 and 5 are rudimentary in Ruminants, lacking in Tylopoda and *Moschus*, the corresponding metatarsals being rudimentary in Ruminants, absent in others. The feet have at most four digits, 2 and 4 with hoofs in swine, although not reaching
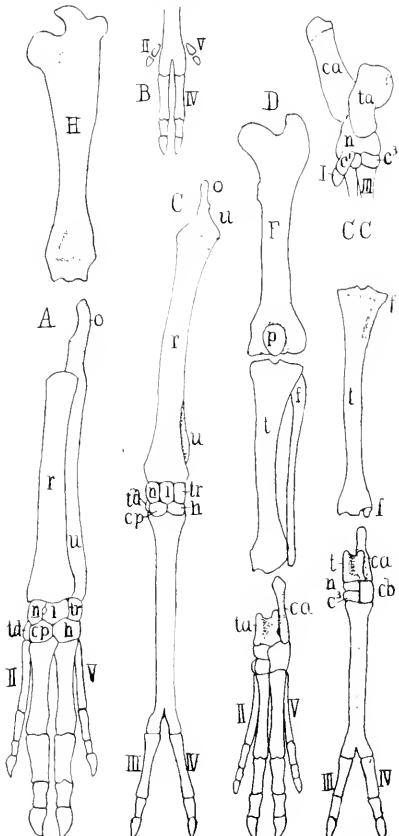
FIG. 322.—Feet of Artiodactyls: *A*, Fore foot of *Phacochœrus; B*, fore foot of *Oryx; C, CC*, fore and hind feet of *Auchenia; D*, hind foot of *Sus* (Weber, '04). Letters as in figure 321.

the ground. *Dicotyles* has 5 reduced, leaving but three digits in the hind foot. Tylopoda, giraffes and some antelopes have lost all but 2 and 3. Tylopoda have no true hoofs and the digits bear horny pads, and in these and in *Hippopotamus* a part of the manus rests on the ground. Many extinct Artiodactyls have somewhat similar semiplantigrade feet.

HYRACOIDEA have slender limbs. The rather long humerus has a large lateral tuberosity and a large fossa for the olecranon. Radius and ulna are strong and

separate; carpus and tarsus are almost perfectly taxeopodous, and each has a centrale. The three middle digits of the manus are subequal; 1 and 5 much smaller, the latter having three phalanges. The axis of the foot is as in Perissodactyls. The femur has a small third trochanter; the fibula is entire and largest distally where it fuses with the tibia and articulates with the talus. The hind feet are three-toed, the hallux being absent and 5 represented by a small metatarsal nodule.

PROBOSCIDIA have the head of the humerus scarcely separated from the shaft by a neck, and no epicondylar foramen. Radius and ulna are separate, the latter complete, its distal end the larger. The carpus (fig. 323) is completely taxeopod; the centrale fuses with the radiale in the young, but the other carpal bones remain separate. Carpale 1 resembles a short metacarpal. The metacarpals and the digits of the semiplantigrade feet are short. The short femur
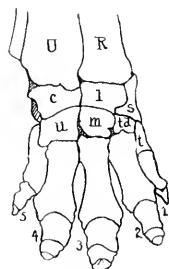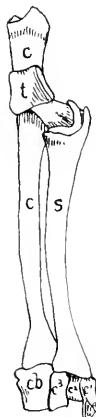
FIG. 323.   FIG. 324.

FIG. 323.—Fore foot of elephant (Flower and Lyddeker, '91). *c*, triquetrum (ulnare); *l*, lunatum (intermedium); *m*, magnum (carpale 3); *R*, radius; *s*, naviculare (radiale); *t*, *td*, trapezium and trapezoid (carpalia 1 and 2); *U*, ulna; *u*, hamatum (carpalia 4 and 5).

FIG. 324.—Tarsus of *Tarsius* (Burmeister, Weber, '04). *c*, calcaneus; c^{1-3}, ento-meso-, and ectocuneiformia; *cd*, cuboid; *s*, scaphoid.

has no third trochanter; tibia and fibula are separate, the latter slender and articulating with the calcaneus. The tarsus is almost perfectly taxeopod and the hind feet are very similar to those in front.

SIRENIA have the fore limbs well developed, the hinder pair vestigial or lost. The fore limbs differ considerably from those of whales, with which these animals were formerly associated, in the extent and freedom of the joints. The humerus has the tuberosities distinct in *Halicore* and *Rhytina*, and its lower end has a well-developed trochlea and a moderate olecranon fossa. Radius and ulna, nearly equal, are fused at either end. The manus is nearly normal, most of the bones being separate in *Manatus*, the carpalia largely fused in *Halicore*. The five digits have the normal phalangeal formula. No traces of a free hind limb exist

in the living genera, but *Halitherium* has a vestigial femur articulated in a distinct acetabulum.

PRIMATES have the appendages more primitive than in most mammals. The femur has the entepicondylar foramen in Lemuroids and many new world monkeys, none in the old world species. The tuberosities are little developed, but the olecranon fossa is deep in the monkeys of the eastern hemisphere. Radius and ulna are separate and capable of extensive rotation, especially in the higher genera. Radiale and intermedium are distinct, as is the centrale in most species; in some (gorilla, chimpanzee and some lemurs) it is fused with the radiale. A radial sesamoid is common and the pisiforme is long in the higher genera. The carpus articulates with both forearm bones, except in Anthropoids and man. The five digits are very variable in form and size in lemurs, in correlation with their arboreal habits. In all Primates the thumb, and in most species, the great toe are opposible to the other digits. The pollex is always short. The femur has a small trochanter except in apes and monkeys. The humerus has a small neck between shaft and the hemispherical head. Tibia and fibula are separate and there is a slight rotation of the crural bones. In lemurs calcaneus and centrale are long, especially in *Tarsius* (fig. 324). Of the five digits the hallux is short and the fourth is the longest in lemurs.

Here may be mentioned, to complete the list of vertebrate bones, the **os priapi (penis bone),** an ossification arising in the connective tissue of the corpus spongiosum of the penis. It occurs in a few Insectivores and in many rodents, Carnivores and bats. Sometimes it is a simple rod; it is bent in Procyonidæ, grooved in Canidæ (the urethra lies in the groove) and forked in bats.

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